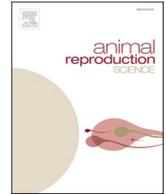




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Review article

Reproduction of male reindeer (*Rangifer tarandus*)

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ABSTRACT

The present review provides a comprehensive assessment on the basic aspects of the reproduction of the Rangifer male with a special focus on pubertal development, and the seasonal dynamics of gametogenesis, androgenesis, antler cycle and other physiological and behavioural characteristics of the rutting male. A greater understanding of the reproductive physiology of the males is needed to improve existing management strategies of semi-domestic stocks in the changing climate and to develop species-specific assisted reproductive technologies for improving the *in situ* and *ex situ* conservation programs to preserve endangered subspecies as well as to facilitate the transfer of genetic resources between fragmented wild or semi-domestic populations.

1. Introduction

Rangifer (*Rangifer tarandus*), reindeer in Eurasia and caribou in North America, and humans have a long-shared history. During the “Age of Reindeer”, which peaked around 11,000–18,000 years ago, humans pursued and hunted reindeer and caribou throughout the northern hemisphere. After the last period of glaciation, Rangifer moved northward, and humans followed. At the present, there continues to be close Rangifer-human interactions in the arctic regions. Semi-domestic reindeer are kept primarily for meat production, but also for transportation, fur, leather, and antlers. Wild reindeer and caribou are still hunted in Eurasia as well as in Alaska and Canada (Vitebsky, 2005).

Semi-domesticated reindeer are considered to be in an early phase of domestication (Clutton-Brock, 1999). The origin(s) of reindeer pastoralism, where, when and why, has been, and still is, debated (Laufer, 1917; Røed et al., 2018). Animals are normally kept in extensive natural conditions with relatively little human interaction and with fecundity being similar to that of animals in their natural habitat with there being 80%–90% pregnancy rates (Mossing and Rydberg, 1982; Ropstad, 2000). The reproductive physiology of the species, therefore, has not been a focus of studies. Intensification of the management regimens, however, can be expected in the future, which is a primary reason for the need of a greater understanding of the basic aspects of reproduction in reindeer. Furthermore,

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it is noteworthy that any information based on the extensively managed semi-domestic reindeer may be applicable to wild, endangered populations (Ropstad, 2000). Attention has mainly been on the reproduction of the females (as reviewed by Ropstad, 2000). There is, however, need for a similar review on the basic reproductive physiology of Rangifer males. The main aim for composing the present review is to provide a comprehensive overview of the basic aspects of the reproduction of the Rangifer males (with a focus on endocrinology, sperm production, antler development and other physiological characteristics).

Rangifer is a classic ice age relict animal with a short, intense rutting season (Geist, 1998). The reproductive cycle in Rangifer females is modulated by seasonal changes during the year, with photoperiodic effects predominating in this regard. The seasonal conditions where Rangifer are located are harsh during the winter and lush in the summer periods with there being an abundance of high-quality forages during the summer. The rut is in the autumn, concurring with the decreasing photoperiod (Ropstad, 2000). There have been marked adaptations of Rangifer to the high latitudes (Stokkan et al., 1994, 2007). Although it may be tempting to apply the relevant information available on other Cervids (especially because there are excellent reviews on reproduction of red deer, *Cervus elaphus*, by Garde et al., 2006; Pintus and Ros-Santaella, 2014; Asher, 2018) to reindeer/caribou, Rangifer have several unique traits, as subsequently described in this review, which highlights the need for this species-specific review. Furthermore, even within the species, the different ecotypes, and subspecies have different reproductive characteristics. For example, barren ground caribou (*Rangifer tarandus groenlandicus*) and the tundra reindeer equivalent (*Rangifer tarandus tarandus*) have extremely short synchronized mating seasons which does not occur in the woodland/taiga subspecies, (Mossing and Rydberg, 1982; *Rangifer tarandus fennicus*, *Rangifer tarandus caribou*, Geist, 1998). Unfortunately, some of the most comprehensive studies on the reproductive physiology of the male reindeer have focused on rather atypical subspecies. These include the Newfoundland caribou (Bergerud, 1975), which is a distinct and isolated subspecies, a unique island form (*Rangifer tarandus terraenovae*; Geist, 1998); or a subspecies in atypical environment, such as the Norwegian semi-domestic reindeer transferred to the sub Antarctic island of South Georgia (Leader-Williams, 1979a).

In the following sections, there is a comprehensive review of the seasonal dynamics of the testicular functions, both endocrine and gametogenetic, of male Rangifer with consequential associations with the antler cycle and other physiological and behavioural characteristics of the male during the rutting period.

2. Anatomy of the reproductive organs of male reindeer

Genitals of a male reindeer include two symmetrical testicles and two epididymides on the craniomedial aspect of the testicles inside the scrotum, two *vasa deferentia*, two ampullae, a prostate, two seminal vesicles, urethra inside the penis and a prepuce (Fig. 1a and c). Whether or not a male reindeer has a bulbourethral gland has not been ascertained. Testicles are oval in shape and depending

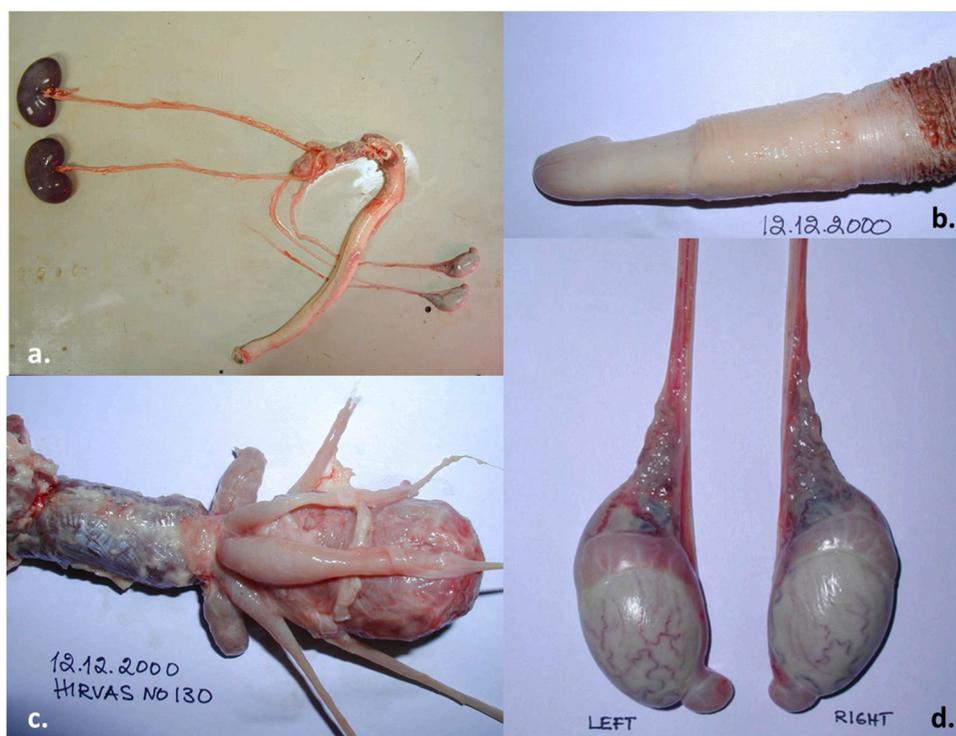


Fig. 1. (a) Urogenital organs of a male reindeer; (b) Glans penis and a short *processus urethrae* on the side of the tip of the penis; (c) Accessory sex organs of a male reindeer; *Uterus masculinus* as well as the left ureter and left *vas deferens* are torn; (d) Testicles and epididymides of reindeer; Organs are from two reindeer slaughtered in the middle of December at the end of the breeding season. Photos by Heli Lindeberg.

on the time of the year, with weight of a single testicle varying from approximately 15 (Meschaks and Nordkvist, 1962) to 90 (Zhinunov, 1968) g in mature males. The epididymis has a small caudal section (Fig. 1d) in comparison to the size of the testicle.

Accessory sex glands (ampullae, prostate and seminal vesicles) are relatively small in reindeer. Reproductive organs of two reindeer males were studied (Lindeberg, unpublished observations) and one male had a *uterus masculinus* (Fig. 1c) between the ampullae. This uterus-like structure has been reported to be a component of reproductive organs of more than 80 % of European bison bulls (Świeżyński, 1968; Skobowiat et al., 2010) and being present in animals of the genus, Rangifer (Walker, 1922). The *uterus masculinus* in Fig. 1c contained a light-coloured secretion and appeared to have an opening to the urethra. This persistent form of a Müllerian duct in European bison and males of other species including humans (Panasiewicz et al., 2015) generally degenerates during the foetal development.

The penis of male reindeer is a fibro elastic organ which does not have a distinct *flexura sigmoidea* that is typical in cattle (Rowell and Blake, 2018). The tip of the glans penis has a short *processus urethrae* (Fig. 1b). The penis is rather short (Fig. 1a) without the *flexura sigmoidea*. In male reindeer, therefore, there are some physiological developmental changes needed to achieve the ability to copulate. The non-erect penis, therefore, has to have the capacity for protrusion before the mating season (Meschaks and Nordkvist, 1962) and the belly drawn in (Preobrazhensky, 1968) in order to facilitate successful copulation. Also, during semen collection with use of electro ejaculation of anaesthetized males, exteriorizing of the penis from the prepuce is generally more successful in the active months of the breeding season (October to November – early December) because these physiological changes have occurred.

3. Basic reproductive physiology of the reindeer male

3.1. Puberty

Males are pubertal when both the processes of androgenesis (endocrine activity) and gametogenesis occur resulting in spermatozoa being transported into the tubules of the reproductive tract (Lincoln, 1971a; Leader-Williams, 1979a). Results from early studies on reindeer and caribou were inconsistent with regard to this aspect of reproduction. In the comprehensive PhD-thesis, McEwan (1963) reported that barren ground caribou were sexually mature at the age of 17–18 months, based on the histological findings of evaluations of testes and epididymides. Endocrine functions may already be detectable at a much younger age. Whitehead and McEwan (1973) reported a marked increase of plasma testosterone concentrations in prepubertal caribou x reindeer hybrid calves. Borozdin (1963) indicated that reindeer were pubertal by the age of 15 months, but the complete development of testes did not occur until the age of 2 ½ years of age. The sex glands began to produce spermatozoa only when the individuals were pubertal at 15 months of age. When males were 1 ½ years of age, weight of gonads and epididymides were 21.2 % and 37 % less than weight of gonads and epididymides in reproductively mature animals.

Leader-Williams (1979a) reported that male reindeer transferred from Norway to South Georgia were pubertal at the age of 4–8 months of age because this age group had testicular weight changes, gonadal androgen production and spermatogenesis. Other sexual characteristics such as rutting odour production or displays of rutting behaviour were not observed. If such characteristics are included in the definition of puberty, reindeer males do not reach puberty by the time they are 1 year of age. In older males, however, by 1 ½ years of age secondary sexual characteristics have developed such as testicular functions and sexual behaviour. The development of fully functional testis at this age may lead to important consequences resulting in males that are 1 ½ years of age mating with non-pregnant females at the end of the short and intense rutting period, when adult males may not have the physical capacity as a result of energy utilization earlier in the rutting period to continue to mate with females that are in oestrus (Leader-Williams, 1979a) as also documented by Holand et al. (2006). The reproductive contribution of Rangifer males that are 1 ½ years of age depends on the sex ratio of a population. Rangifer males are less active where the proportion of prime-age males is greater and the competition for mating with females is more intensive (Mysterud et al., 2003). Skjenneberg and Slagsvold (1979) reported that males do not generally mate with females until they are 1 ½ years of age, however, in experimental conditions when there was mating with females by males of this age group fertilization rates were 90%–95% (Lenvik et al., 1988). In Rangifer populations in the natural habitat, males rarely have dominant sexual behaviour before 4 years of age. Young males have less body fat compared to adults. There is mainly partitioning of energy into somatic growth, and therefore they have limited resources for reproductive functions (Kojola, 1991). In a study of a large population of wild reindeer where there was a natural sex ratio (0.45 male/female), there were, however, several 1 ½ year old males that mated with more females than reproductively mature males, which results because of different mating behaviours of the younger as compared with reproductively mature males. For males to have a greater social rank and defence of their mating groups from other competing males, a large body size and antlers are important. In sub adult males, there are other traits, like sneaking behaviour and endurance that are advantageous for mating with females during the rutting period (Røed et al., 2005).

Ryg (1984) reported there were similar androgen hormone profiles in reindeer calves as those reported by Whitehead and McEwan (1973) and Leader-Williams (1979a), however, there was a close correlation between body weight at 6 months of age and the maximal testosterone concentration of the same individual at 1 ½ years of age. Animals with *ad libitum* access to pelleted reindeer feed were larger at maturity and had significantly higher peak testosterone concentrations, both as calves and at 1 ½ years of age than when animals had restricted access to supplementary feed. Supplementary feeding of male calves and the associated greater body weight gains, therefore, may result in an increased value as breeding animals at least in certain commercial herding and grazing systems.

3.2. Gametogenesis in the adult

Reproductively mature reindeer, as with other seasonally breeding Cervids, have an annual cycle of testicular maturation and

involution (Meschaks and Nordkvist, 1962; McEwan, 1963; Whitehead and McEwan, 1973; Leader-Williams, 1979a). These marked changes were described by Lincoln (1971b) as “annual puberty” in red deer. Approaching the rutting period, reindeer males have distinct morphological, physiological and behavioural changes such as growth of the scrotum, mane and neck muscle development; antlers are cleared of velvet; and they become more behaviourally aggressive (Preobrazhensky, 1968; Skjenneberg and Slagsvold, 1979; Mossing and Damber, 1981). There are, however, very few studies where there is a description of the annual histological changes in the testes and epididymis of the mature reindeer (Meschaks and Nordkvist, 1962; Borozdin, 1964; Leader-Williams, 1979a) or caribou (McEwan, 1963).

From January to March, testes are small (weight approx. 15 g) and interstitial tissue is smaller with only a few Leydig cells present. Tubular epithelium is less with there being only one cell layer with a few spermatogonia, and occasionally a single primary spermatocyte. In April, the tubular epithelium becomes more organized, with there being an increasing number of primary spermatocytes and in some tubules active spermatogenesis can be observed. During the summer, there is a gradual regeneration of the testicular epithelium. In August, the epithelium becomes well organized and the interstitial tissue is more abundant. The regeneration of the testicular epithelium is complete in September and testes weigh about 50 g. After the rutting period, by late November, there is an acute regression of the testicular epithelium which is complete by late December (Meschaks and Nordkvist, 1962). Leader-Williams (1979a) reported similar seasonal changes (with a complete seasonal reversal due to the transfer of the animals to the Southern Hemisphere) in testicular and epididymal weights and an incrementally greater weight cycle change in association with increasing age. Results from histological investigations indicated the production of spermatids occurred about 1 month before the rutting period started, at the same time there were spermatozoa detected in the epididymis. In 1 ½ year old males, however, such changes occurred at the beginning of the rutting period. Production of spermatids ceased about 3 months later after the rutting period in males that were 1 ½ years of age and in younger adult males, probably earlier in adults older than 3 years of age. The results from evaluation of the area of the seminiferous tubules in histological specimens indicated there were similar cyclical changes, but the amplitude of this cycle did not increase with age.

Borozdin (1964) collected samples from 192 males between 1959 and 1962 and reported similar testicular dynamics as those previously described in this review: with complete spermatogenesis occurring from August to October. In November, the process of “physiological atrophy” was initiated, and was maximal during the March to April timeframe. During this period, there was no detection of germ cells, except for spermatogonia. During May and June, there began to be development of testicular functions. At the age of 2 ½ years, during the period of active spermatogenesis, the average weight of gonads and epididymidae were 71.8 and 7.3 g, respectively. The volume of the ductus epididymis was 2.7 mL, and the length was 85 mm. The transit period for spermatozoa through the ductus epididymis was 11 days.

McEwan (1963) reported that testicular development and involution in caribou was of a similar annual pattern but major changes happen later. The growth of the testes starts in May, and size is maximal in late September and October with there being a rapid regression in December, when the size of the testes decreases and the tone of the testes is more flaccid. Testicular size increases from the non-breeding season to the rutting period by approximately 63 %, which is mainly due to the increase in tubular diameter. In the developing testis, spermatogenic functions increase. From mid-September until early December, spermatozoa are present in the tubules. After the end of the breeding season, tubules contain only a layer of spermatogonia and Sertoli cells, and epididymides are in a quiescent state (McEwan, 1963).

Reindeer have considerably smaller ejaculate volumes (0.5 compared with 4 mL), total number of ejaculated spermatozoa (2.3 compared with 8×10^8) and larger sperm concentrations (460,000 compared with 200,000 sperm cells/ μ l) than red deer (Glover, 2012). The findings indicate there is a much smaller sperm storage capacity which was not anticipated because reindeer males have relatively large testes which indicates intensive sperm competition (Clutton-Brock et al., 1982; Lüpold et al., 2020). One can speculate that there is an evolutionary advantage for the smaller cauda with there being a lesser detrimental effect of extremely low temperatures, somewhat similar to yaks, which have hairy scrotum that is smaller than in other bovine species (Wiener et al., 2003).

3.3. Androgenic functions in the adults

The first study on the endocrine aspects of the reindeer male sexual cycle was conducted by Meschaks and Nordkvist (1962). As an indirect measure of the steroidogenesis throughout the annual reproductive cycle, the concentrations of the Zimmermann chromogen, indicating the concentrations of androgen metabolites (Rudd, 1983), were measured from crude urinary extracts. All males ($n = 3$) that were evaluated had similar variations: Zimmermann chromogen concentrations were less during the winter, increased during the spring-summer (relatively greater concentrations in April-May) and were maximal during the autumn months.

Whitehead and McEwan (1973) quantified plasma testosterone concentrations in reproductively mature reindeer ($n = 2$) and caribou ($n = 2$) to determine seasonal hormone concentration changes during a 12-month period. There were similar seasonal patterns with plasma testosterone concentrations being basal during the summer (about 1 ng/cm³), increasing in August to being maximal at a 30–60 ng/cm³ concentration in September in reindeer. In caribou, the maximal concentrations were similar, however, these maximal concentrations occurred about 1 month later than in reindeer. There was a rapid decrease from these maximal concentrations to 1 ng/cm³ by mid-October to early November and concentrations remained basal until August of the subsequent year. One of the reindeer males had a second testosterone peak in May, which is consistent with the findings of Meschaks and Nordkvist (1962).

In a subsequent study, Whitehead and West (1977) quantified testosterone production and seasonal changes in metabolic clearance rates for testosterone. Seasonal differences in the plasma concentrations of testosterone are related, not just to the production rate, but to the rate of metabolism and volume of distribution as well. During the rutting period, the metabolic clearance rates were less than expected, which can be explained by a greater binding capacity in plasma during the rutting period.

There has been questioning (Stokkan et al., 1980) of the methods used in the abovementioned studies because testosterone concentrations were determined from single samples. To investigate the short-term variations in plasma testosterone concentrations, the blood samples were collected during the rutting period at hourly intervals from three reindeer males for 48-h. Furthermore, blood from one male was collected at 20 min intervals for 3 h for a total of 27 h with 3 h periods between sampling times. There were correlations of these values with those of the plasma concentrations of LH quantified from the same blood samples. The testosterone concentrations were maximal with 3–4 h intervals between when these maximal concentrations were detected, without a distinct diurnal pattern being evident. Mean LH concentrations differed between individuals and were correlated with the social rank of the male. The LH concentrations were basal with only small, non-significant variations. Results when there was more frequent sampling indicated that there was a closer temporal relationship between LH and testosterone concentrations, with there being LH episodic releases preceding episodic increases in testosterone concentrations. The lesser LH and greater testosterone concentrations during the rutting period can be explained by the greater negative feedback of testosterone on LH.

Bubenik et al. (1997) evaluated the seasonal changes in reproductive hormones (LH, FSH, testosterone, 17 β -estradiol, progesterone, and prolactin) in adult reindeer males ($n = 5$), adult non-pregnant females ($n = 4$) and adult pregnant females ($n = 5$). There was collection of peripheral blood samples at 3-week intervals throughout a year. In males, there were simultaneous increases in LH and FSH concentrations in April, indicating the activation of the reproductive system. The concentrations of LH were greatest in May and there were decreases that started to occur until the time of the rutting period. Concentrations of FSH were greatest about 1 month after those for LH. Testosterone concentrations were greatest in the August-September time period, approximately 3 months after there were the greatest concentrations of LH. There were the greatest LH, FSH and testosterone concentrations in the most physically aggressive males with these males having the largest antlers which is consistent with the findings of Stokkan et al. (1980). During the rutting period, males had greater 17 β -estradiol concentrations than pregnant females before parturition. Prolactin concentrations were greatest in the May-June time period, with females (both pregnant and barren) having greater concentrations than males.

3.4. Antler cycle

The antler development of reindeer has several unique aspects compared to other Cervids, the most striking difference being that females also grow antlers. Another interesting aspect of the reindeer antler cycle is that between casting the old and growing a new antler, there is a period of several months. (Leader-Williams, 1979a).

In most of the studies where there was a focus on the endocrine aspects of the reproductive cycle of reindeer, there was consideration of the antler cycle as well. Meschaks and Nordkvist (1962) collected corresponding data in 20 reindeer herding districts and reported latitude, environmental conditions, climatic variations and the age of the animals all had effects on the seasonal pattern of the reindeer antler cycle. Furthermore, they noted that reindeer calves developed a straight, unbranched antler well before sexual maturity. The initiation of the male annual antler growth coincides with the initiation of the testicular epithelium regeneration with the first antler buds appearing in the March-April time period. During summer, antlers fully develop, and velvet shedding starts between early August and early September. After removing the velvet from the antler, males become more aggressive and even dangerous to humans. Antler casting varies greatly, from November to May the next year. Older males usually shed their antlers earlier than young or under-nourished animals (Meschaks and Nordkvist, 1962). This observation was supported by the results of Leader-Williams (1979a), who also noted that there were earlier occurrences of the annual cyclic changes in antlers in older than younger animals. Testosterone has functions in antler development but there may be a second factor/hormone which can also affect the cycle of antler changes in females. From results in a subsequent study, Leader-Williams (1979b) reported the antler cycle of cryptorchidic males was similar to non-cryptorchidic males, therefore, this abnormality has a minimal effect on antler development compared to that of other deer species. Castrated males (and spayed females) may develop antlers that are of typical structure, however, the method of castration has an effect on antler development. If the castration does not involve the complete removal of testicles ('weak' castration), antler development, velvet cleaning and antler shedding will be similar to that of the reproductively-intact animals. If castration involves complete testis removal ('hard' castration), the velvet will usually remain desiccated on the antler until antler casting, which occurs later compared to that of reproductively intact males. Furthermore, the antler structure is different, being more spongy in 'hard'-castrated animals (Tandler and Grosz, 1913, cited by Meschaks and Nordkvist, 1962).

As a result of a study on the antler development in male reindeer that were 1 ½ years of age, Ryg (1983) reported that testosterone has a similar qualitative effect on antler growth as in other Cervids, but does not have as great an effect on antler calcification and velvet cleaning. It was suggested that there is an antler growth stimulation (or inhibition) factor which can be overridden by testosterone in males (as suggested by Leader-Williams, 1979a; as well).

Results from studies on the antler cycle of female reindeer (Lincoln and Tyler, 1994, 1999) support the theory that testosterone produced by the testes is not essential for the seasonal development of the antlers but has a predominant effect on the timing of the antler cycle, serving to synchronize these hormonal actions on antler development with the stages of the reproductive cycle. It was suggested (Lincoln and Tyler, 1994) and later experimentally verified (Lincoln and Tyler, 1999) that there were actions of 17 β -estradiol in the regulation of the antler cycle of female reindeer. Bubenik et al. (1997) suggested that 17 β -estradiol may act as a secondary steroid in the antler development of males.

The antler cycle is different in male and female reindeer (Lincoln and Tyler, 1994) because females cast their antlers later than reproductively mature males. This can be a consequence of sex-specific competition. Males compete with each other during the rutting period for access to females, while females have to compete with each other and younger males for food during winter, while they still retain their antlers (Geist, 1998). In both cases the antlers have important functions as indicators of social rank as well as being functional weapons (Barrette and Vandal, 1986; Holand et al., 2004)

3.5. Rutting behaviour

The polygynous mating system in Rangifer is based on the capacity of males to express behavioural, and mating posturing that result in impregnation of more than one female during the short rutting period when there is marked physical activity. The reproductive characteristics of reindeer are reflected in the sexual size dimorphism that is predominant in males (Geist, 1998) and resulting variation in reproductive success (Røed et al., 2002, 2005). These findings exemplify the importance of sex-specific sexual selection where males are risk prone and conspicuous. Indeed, numerous behavioural and physiological mechanisms are associated with the highly synchronous male-female mating season that results in male-male competition for priority of access to females.

The timing in onset of the breeding season varies and can first be ascertained by characteristics of adult and well-nourished males. By the end of August, adult males begin cleaning their antlers of velvet. Later, 2 ½ and 1 ½ year-old males begin cleaning their antlers. In the first half of September, all indications are that adult males have developed the characteristics and functions for reproduction necessary for rutting. They grow a mane, and the neck thickens during this period. From the beginning of the rutting period (usually in the end of September or early October), the males become physically active, seek out females, and have fierce clashes with other males (Preobrazhensky, 1968). Caribou males initiate rutting 4–6 weeks later than reindeer, even when they are maintained at the same site and are fed the same diet (Whitehead and McEwan, 1973). Systemic testosterone concentrations begin to increase in August or early September (Stokkan et al., 1980; Bubenik et al., 1997), depending on latitude and grazing conditions, and as a result there is antler ossification and cleaning. This correlates with increasingly aggressive behaviours where the reproductively mature males are competing for priority access to females through behavioural actions, chases and ultimately fights. These preliminary behavioural bouts may induce the onset of ovarian functions in females, as reported in other ungulates, (e.g., sheep, Fabre-Nys et al., 2015). Results from earlier studies indicated that reindeer females need physical contact with a male for behavioural oestrus to occur (Rainio et al., 1997). This “male effect” has been questioned and Shipka et al. (2002), who concluded that male presence is not necessary for the initiation of reproductive cycles in females, although when males are placed with females there was induction of behavioural oestrus.

The reproductive responses lead to the subsequent phase of reproductive patterns where adult males attempt to control a group or individual females by dominance display and herding. There is the greatest mating activity during the rutting period (~10 days), during which almost all females are mated and conceive (Holand et al., 2003). Dominant males express many behavioural characteristics that are consistent with rutting, the most conspicuous being vocalizations (grunting), bush trashing, scent marking, herding females and chasing other males (Tennenhouse et al., 2012). Dominant males remain in close proximity to the females of their mating group and these males are always alert and move among females where there are expressions of behaviours that allow for extent of receptiveness to be determined with the expression of the flehmen response, with head held low and frequently sniffing the females' vaginal area and places where females have urinated. When an oestrous female is detected, the courtship, which may last only minutes or continue the whole day, depending on the females' oestrous state, starts with male grunts and flehmen responses, steadily approaching females from the side and back. A few minutes before male acceptance, the female's behavioural pattern changes with expression of an increased interest in the male by following him more closely (Holand et al., 2012). The male will make attempts to mate with females that have these types of behavioural responses. Often there will be several attempts at mounting before the female takes on a stationary stance and stands to be mounted by the male. The copulation period is for only a few seconds, and the dominant male loses interest in the female with which he mated and starts searching for other females that are in oestrus, whereas, the female attempts to avoid being mated by males that are less dominant in the reproductive hierarchy (Holand et al., 2006).

During periods when rutting expression is maximal, food intake by males decreases and almost ceases during period when rutting is maximal, representing a substantial energetic cost to dominant males (Barboza et al., 2004). Dominant adult males may utilise as much as 25 % of their body energy reserves during the rutting period (Mysterud et al., 2003). These uses of energetic reserves for reproductive functions increases the likelihood of a male transmitting his genes to subsequent generations, with as many as 30 calves being from a single dominant male as a results of mating that occur during a single rutting season (Røed et al., unpubl. data). The dominant characteristic is obviously an important aspect of reproductive fitness (Røed et al., 2002). Males, therefore, become physically exhausted by the end of the rutting period. In comparison, young males devote most of their time to foraging and are able to maintain their body mass during the rutting period (Tennenhouse et al., 2012). The elusive approaches of these non-dominant males lead to mating opportunities during the latter part of the rutting period (Røed et al., 2007). The mating behaviour of these subordinate males is less well developed and they do not have the capacity for controlling larger number of females. If adult males, however, are not present in the herd males that are 1 ½ years old mate with females and conception can occur as a result of matings. Ratios of one male to 10 females are adequate to ensure a pregnancy rate of about 85 % (Holand et al., 2003).

3.6. Other aspects

Other physiological changes associated with rutting, and coinciding with the increase of androgen concentrations, are the swelling of the neck muscles and the enlargement of the neck girth, which rapidly decreases after the rutting period (Lund-Larsen, 1977; Inga, 1984; Kiessling et al., 1987), growth of the mane and scrotum, and a change in breath and urine odour (Mossing and Damber, 1981). Aroused males spray the strongly odoriferous urine onto their hind legs while trampling (Espmark, 1964; Mossing and Damber, 1981), but this behaviour is only typical of older males because males that are 1 ½ years old do not express this pattern of urination (Kojola, 1991). The changes in the size of neck muscles indicate there is a close correlation with testosterone concentrations in adult males, while such correlation was absent when there were these evaluations in younger males (Inga, 1984). The neck muscles are actually considered as secondary sexual organs in male Cervids (Lincoln, 1971a).

4. Conclusions, further directions for future studies

Although there are generally excellent reproductive outcomes in extensively managed semi-domestic reindeer herds, a greater understanding in the reproductive physiology of the males is an important aspect for improving management strategies of semi-domestic stocks in a changing climate and to develop tailored methods for conducting the Assisted Reproductive Technologies (ART). Because of the limited knowledge of functional reproductive anatomy of reindeer, there needs to be further basic investigations (for example, to clarify the functions of the *uterus masculinus* and the absence of bulbourethral glands). Furthermore, species specific ART can provide help with the *in situ* and *ex situ* conservation programs to save endangered subspecies from extinction, as well as to provide easier gene transmission between fragmented wild or semi-domestic populations.

CRedit authorship contribution statement

Sz. Nagy: Writing - original draft, Writing - review & editing. **H. Lindeberg:** Visualization, Writing - original draft, Writing - review & editing. **E. Nikitkina:** Writing - review & editing. **A. Krutikova:** Writing - review & editing. **E. Smith:** Writing - review & editing. **J. Kumpula:** Writing - review & editing. **Ø. Holand:** Conceptualization, Funding acquisition, Project administration, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

Authors have no competing interests to declare.

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