Role of oestradiol in the regulation of the seasonal antler cycle in female reindeer, *Rangifer tarandus*

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Reindeer (or caribou), *Rangifer tarandus*, is the only extant species of deer in which females as well as males normally develop antlers that are cast and regrown each year. This study investigated the role of ovarian oestradiol in the regulation of the seasonal antler cycle in female reindeer. Ovariectomized Norwegian reindeer living outdoors in northern Norway (69°N) were treated with continuous-release subcutaneous Silastic implants containing oestradiol, which maintained the blood concentrations of oestradiol within the physiological range for the mating season from June to October–November. The treatment with oestradiol induced the synchronized maturation of the antlers and rapid cleaning of the velvet-like skin in August–September in the ovariectomized reindeer, a pattern very similar to that observed in ovary-intact controls living under the same conditions. The removal of the steroid implant in October–November caused the premature casting of the antlers in early winter in two of five animals, while the remainder cast at the normal time in spring; this response was seen whether the animals had received one or two oestradiol implants in autumn. The antlers developed by the ovariectomized, oestradiol-treated females were significantly heavier and carried more branches than the ovariectomized animals without oestradiol replacement, and were marginally heavier than the antlers of intact controls. These results support the view that oestradiol is the biologically active steroid secreted by the ovary in intact female reindeers that induces the normal development of the antlers. Oestradiol stimulates the growth and mineralization of the antler bone, the cleaning of the velvet, and suppresses the casting of the hard antlers. This endocrine control ensures that the hard antlers, which function as weapons, are retained throughout the autumn and winter when the females are normally pregnant and when competition between females over food in the snow is most intense; hence there is a reproductive advantage to explain the evolution of antlers in females.

Introduction

The hormonal regulation of the seasonal antler cycle in female reindeer (or caribou), *Rangifer tarandus*, is poorly understood. The circulating concentrations of testosterone are low throughout the year in females, so it is unlikely that testosterone regulates the antler cycle, as it does in males (Leader-Williams, 1979; Ryg, 1983). In females, the cleaning of the velvet from the antlers in autumn coincides with the onset of ovarian activity at the start of the mating season and the hard antlers are retained throughout the winter. Pregnant animals normally cast the old antlers soon after calving in spring, while non-pregnant individuals cast a few weeks earlier (Espmark, 1971; Gagnon and Barrette, 1992). Experimental studies have shown that ovariectomy in

October, once the hard antlers have developed, causes premature casting of the antlers within as little as 4 weeks (Lincoln and Tyler, 1994). However, long-term ovariectomized females continue to develop and cast a new set of antlers each year, although the antler cycle is permanently abnormal since cleaning of the velvet occurs 1–3 months later than in intact females and is often incomplete, and the antlers tend to be readily broken in winter (Tandler and Grosz, 1913; Lincoln and Tyler, 1994). Overall, these observations indicate that increased secretion of ovarian hormones in autumn and winter plays an important role in controlling the seasonal development of hard antlers in female reindeer. The ovarian hormone, oestradiol, is a possible candidate since the circulating concentrations of oestradiol increase in autumn coincident with cleaning of the antlers (Lincoln and Tyler, 1994) and, on the basis of studies in other ungulates (white-tailed deer: Harder and Woolf, 1976; Plotka *et al.*, 1977; domesticated sheep and goat: Challis and Linzell, 1971), oestradiol secretion is likely to be increased during

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pregnancy, which would account for the association between the time of parturition and antler casting in reindeer. Pharmacological doses of oestradiol induce calcification of the growing antler and cleaning of the velvet in males of other species (Goss, 1963, 1968; Fletcher, 1978; Bubenik, 1990). In addition, in female red deer (*Cervus elaphus*), where antler growth has been provoked by treatment with testosterone and local trauma to the antler pedicles, treatment with high concentrations of oestradiol or stilboestrol in autumn induces cleaning of the velvet and the subsequent casting of the hard antler (Jaczewski, 1990), although this does not occur in response to physiological concentrations of oestradiol in autumn in ovary-intact females (Lincoln, 1984).

The aim of the present study was to investigate the hypothesis that oestradiol is the important endocrine regulator of the antler cycle in female reindeer, by recording long-term changes in ovariectomized female reindeer treated chronically with oestradiol at physiological concentrations from June to October–November. The prediction was that treatment started during the early antler-growing phase would induce full maturation of the antlers and cleaning of the velvet, as it does in normal intact animals, while the sudden cessation of treatment in late autumn would trigger premature casting of the hard antlers.

Materials and Methods

Animals

Observations were made on female Norwegian semi-domesticated reindeer from January 1989 to May 1995. The animals were maintained outdoors in adjacent enclosures at the Department of Arctic Biology, University of Tromsø, Norway (69°N, 19°E), and were given a concentrated pelleted diet RF-71 (Jacobsen and Skjenneberg, 1979) or RF-80, with occasional supplies of lichen, and with water or snow *ad libitum*.

Experimental group

The experimental group consisted of five long-term ovariectomized female reindeer in which the antler cycle had been recorded since the time of ovariectomy in October 1989 (adult at ovariectomy, $n = 4$; Lincoln and Tyler, 1994) and May 1989 (juvenile at ovariectomy, $n = 1$; Lincoln and Tyler, 1992) until the start of the treatments with oestradiol in 1993. The animals were 4–7 years old in June 1993 (mean body weight: 81.4 kg).

In Expt 1, the ovariectomized females were each given one Silastic implant (Dow Corning, Midland, MI) containing oestradiol for a period of 4 months in summer and autumn of 1993. The treatment with oestradiol was started on 21 June 1993 when all the ovariectomized animals were regenerating new antlers in velvet (old antlers cast 63–87 days earlier), and the treatment was ended on 21 October 1993 by the removal of the implant. The Silastic implants were constructed by packing powdered oestradiol into 4 mm diameter Silastic

tubing and blocking the ends with Silastic sealant, as described by Karsch *et al.* (1973). Each implant (total length: 30 mm; steroid compartment: 20 mm) was inserted beneath the skin on the inside of the hind leg. The animals were sedated using an i.m. injection of 80–100 µg medetomidine kg⁻¹ body weight to aid the implant insertion and removal; the effect was subsequently reversed using a single injection of 400–500 µg atipamezole kg⁻¹ body weight (Farnos Group, Turku) (Tyler *et al.*, 1990).

In Expt 2, the same five ovariectomized females were treated with Silastic implants containing oestradiol over the summer and autumn of 1994. On this occasion, each animal received one implant on 16–17 June 1994, and a second implant on 19 September 1994; both implants were removed on 21 November 1994. These manipulations were carried out using a local anaesthetic (xylocain; Astra, Sodertalje) injected into the skin at the site of implantation, and not with general sedation. This second treatment protocol with oestradiol was designed to provide a two-phase increase in the circulating concentrations of oestradiol that would mimic more closely the seasonal endocrine changes in intact female reindeer (Lincoln and Tyler, 1994).

In both experiments, the steroid implants were soaked in water for 24 h before insertion to avoid the brief peak in the circulating steroid concentration that follows insertion of an unsoaked capsule. Single Silastic implants of similar size produce mean peripheral oestradiol concentrations of approximately 5 pg ml⁻¹ plasma in a variety of breeds of domesticated sheep (estimated weight 35–50 kg), and maintain a relatively constant release for > 12 months (Karsch *et al.*, 1977; Webb *et al.*, 1985). In the present study, a single blood sample was collected from the jugular vein of each oestradiol-implanted ovariectomized reindeer on 20 August 1993 (one implant) and on 21 November 1994 (two implants), and the plasma was separated and stored until the concentrations of oestradiol were measured by an ultrasensitive assay (Mann *et al.*, 1995). The concentrations of oestradiol were 1.60 ± 0.12 and 3.20 ± 0.19 pg ml⁻¹ plasma (mean ± SEM) for the one and two implant treatments, respectively, which is within the normal physiological range for intact female reindeer in late summer and autumn at the start of the mating season (Lincoln and Tyler, 1994).

Throughout 1993 and 1994, the state of the antlers of the oestradiol-treated ovariectomized reindeer was recorded every week to construct a profile of the annual antler cycle for each individual. Cast antlers were weighed and the volume was determined by immersion in water to calculate the average density. The length of all intact antlers was measured from the tip to the base along the outside curve of the antler, and the total number of branches (points) was recorded.

Control groups

Data for the patterns of antler development and casting, and the size and weight of the antlers in the ovariectomized reindeer from 1989 to 1993 (Lincoln and Tyler, 1994; N. J. C. Tyler, unpublished) were used to characterize fully the seasonal antler cycle of ovariectomized reindeer in the

Table 1. Summary of antler cleaning and casting dates for the three categories of female reindeer, *Rangifer tarandus*

	OVX, no treatment	OVX + oestradiol	Intact non-pregnant
Date first antler begins to clean velvet	19 October $\pm$ 7.1 days ^a	8 September $\pm$ 3.3 days	14 September $\pm$ 5.5 days
Date first antler cast	11 March $\pm$ 20.8 days	13 February $\pm$ 34.5 days	11 April $\pm$ 6.0 days

Values are mean $\pm$ SEM, $n = 5$.

^aSignificantly different from other groups ($P < 0.005$).

OVX, ovariectomized.

absence of steroid treatment (ovariectomy but no treatment). In addition, data on the seasonal patterns of antler development and replacement, and the other antler characteristics were available for five ovary-intact, non-pregnant female reindeer kept in adjacent paddocks at the research institute between 1989 and 1995 (intact non-pregnant group). These animals were of a similar age to the ovariectomized reindeer, and acted as controls living under the same conditions in captivity.

Statistical analysis

Where data on the timing of the antler cycle and other antler characteristics were available for more than 1 year for an individual reindeer, the mean value across years for that parameter was calculated for each individual, and this was used to determine the group mean $\pm$ SEM. For example, the dates of first antler cast for the ovariectomized no-treatment group were based on data from 1990 to 1993; means were calculated for each individual and then for the group. This involved converting to a Julian date and reconvert to a calendar date $\pm$ SEM in days once the group mean had been determined (Table 1). The corresponding values for the overall oestradiol-treated ovariectomized group were based on data from 1993 to 1995, when the animals received the oestradiol implants. Similarly, the dates of first antler cast for the intact group were based on all data available between 1990 to 1995; means were calculated for each individual and then for the group. The differences between the groups for each antler parameter were assessed for significance using analysis of variance (ANOVA) and a one-tailed Kruskal–Wallis test. Since the data for the untreated ovariectomized and oestradiol-treated ovariectomized groups were derived from the same animals, a further statistical comparison between these two treatments was carried out using paired Student's *t* test.

Results

Effect of oestradiol administration on antler cleaning

The annual cycles in growth, cleaning and casting of the antlers in the five ovariectomized reindeer in 1992 (no treatment) and in 1993 (one implant of oestradiol) are illustrated (Fig. 1), along with data for five ovary-intact reindeer in 1992. In the ovariectomized animals receiving no oestradiol, the cleaning of the velvet from the antlers commenced in October and continued gradually over a

period of 1–6 months during autumn and winter. In some individuals, the process was still incomplete by spring and tatters of dried skin were still adherent to the underlying antler bone. The treatment with one oestradiol implant (Expt 1, 1993), starting in June during the early growing phase, resulted in complete and rapid cleaning of the velvet in late August and early September in all animals. This began at least 6 weeks earlier than it did in animals not treated with steroid, and the synchronous cleaning pattern was very similar to that in the intact controls (Fig. 1). Antler maturation was essentially the same in the ovariectomized reindeer treated with oestradiol in 1994 (Expt 2), when a second oestradiol implant was introduced in September just before or during the cleaning of the antlers (Fig. 2).

The statistical analysis confirmed that cleaning of the antlers occurred significantly ($P < 0.005$) earlier in the years when the ovariectomized animals received oestradiol than they did during periods without treatment (Table 1), and the duration of the cleaning process was significantly shorter (7.0 ± 3.0 versus 60.9 ± 13.8 days, for the combined oestradiol-treated ovariectomized versus untreated ovariectomized groups, respectively; $P < 0.001$). There were no significant differences in the timing and pattern of cleaning between the oestradiol-treated ovariectomized reindeer and intact controls (Table 1). The appearance of the antlers of one ovariectomized reindeer before and after treatment with oestradiol is shown (Fig. 3).

Effect of oestradiol removal on antler casting

The oestradiol-treated ovariectomized reindeer were all in hard antler at the time the steroid implants were removed in October–November (Figs 1 and 2). Two of the five animals cast both hard antlers within 38 days of implant removal (implant removal to antler casting: range 21–38 days), while the others retained the antlers until close to the normal casting time in spring (implant removal to antler casting: range 89–161 days). The same animals that cast early in 1993 (after one oestradiol implant), also cast early in 1994 (after two oestradiol implants; Fig. 2), and the same animals that cast at the later date in the first trial cast close to the normal time in spring in the second trial. Overall, the difference between the casting dates in the ovariectomized reindeer, with and without previous treatment with oestradiol, was not quite significant (paired *t* test, $P = 0.07$; Table 1).

The eroded surface at the base of the cast antlers in the oestradiol-treated ovariectomized reindeer was markedly concave compared with the flat or convex casting surface in the intact controls (Fig. 4). The concave pattern characteristic

Fig. 1. The seasonal antler cycle in: (a) five long-term ovariectomized reindeer that received no treatment in 1992–1993; (b) the same five ovariectomized reindeer treated with one subcutaneous Silastic implant containing oestradiol from June to October (horizontal bar $\times 1$) in 1993–1994; and (c) five ovary-intact, non-pregnant female reindeer that received no treatment in 1992–1993. The stages of the antler cycle are shown as periods of growth in velvet (■), cleaning (▨) and hard antler (□), terminating with the casting of the antlers (vertical lines represent individual antlers).

of ovariectomized animals was evident in the oestradiol-treated ovariectomized animals that cast very soon after removal of the oestradiol implants (total period in hard antler: 62–97 days) and those that cast later (total period in hard antler: 197–226 days; Fig. 4 illustrates an example).

Effect of oestradiol on antler size and branching

The antlers developed by the oestradiol-treated ovariectomized animals were significantly ($P < 0.005$) heavier and had a greater number of fully formed branches (points) compared with the antlers developed by the untreated ovariectomized animals, and were marginally ($P < 0.05$) heavier and more elaborate than antlers of the intact controls (Fig. 5). There were no significant differences between the treatment groups in the length and density of the hard antlers (Fig. 5). Breakage of the hard antlers during the winter through contact with fences and during

interactions with other animals was relatively common in the ovariectomized reindeer before treatment with oestradiol (47% annual cycles), but there were no recorded breakages after the supplementary oestradiol and none in the intact controls over the 5 years of observation.

Discussion

The results of the present study support the hypothesis that oestradiol is an important endocrine regulator of the antler cycle in female reindeer. The treatment of ovariectomized reindeer with oestradiol implants restored a relatively normal pattern of antler maturation with rapid and synchronous cleaning of the velvet in autumn. The replacement therapy produced circulating concentrations of oestradiol of 1.25–3.62 pg ml⁻¹ blood plasma, which is within the physiological range for intact females during late summer and autumn at the start of the mating season

Fig. 2. The seasonal antler cycle in two individual long-term ovariectomized reindeer (R3/86 and R6/86) treated with one oestradiol implant in 1993, and two oestradiol implants in 1994. The timing of the treatments is indicated (horizontal bars $\times 1$ and $\times 2$). The stages of the antler cycle are shown as periods of growth in velvet (■), cleaning (▨) and hard antler (□), terminating with the casting of the old antlers (vertical lines represent the individual antlers).

Fig. 3. Photographs of a long-term ovariectomized reindeer (R3/86) on (a) 12 October 1992 with no treatment when the cleaning of the velvet-like skin from the antler was just beginning (total of 11 antler points); (b) 19 August 1993 after 2 months treatment with one oestradiol implant when the new antlers were fully grown (cleaning of the antler velvet began 11 days later; total of 13 antler points); and (c) 23 October 1994 after 3 months treatment with one or later two oestradiol implants when the large hard antlers were fully formed (total of 16 antler points).

(Lincoln and Tyler, 1994). Since the cleaning of the velvet in the intact female reindeer normally coincides with the seasonal increase in secretion of oestradiol from the ovary at the onset of oestrous cyclicity, and the effect can be mimicked by the administration of exogenous oestradiol, it is most probable that oestradiol is the biologically active hormone

that induces the final maturation of the antler to produce the dead, bony antler that functions as a weapon (Lincoln, 1994).

The reindeer is the only species of deer in which females as well as males normally develop antlers, although the antlers of females are relatively small. The species is also unique in that the antlers begin to develop soon after birth, and both

Fig. 4. Photographs of the base of the cast antler from (a) a representative ovary-intact control female reindeer cast in April 1994 showing the flat-convex casting surface, and (b) an oestradiol-treated ovariectomized reindeer (R5/86) cast on 24 April 1994 showing the concave casting surface.

the initial growth of the antlers and their seasonal replacement persists in gonadectomized animals of either sex (females: Tandler and Grosz, 1913; Lincoln and Tyler, 1994; males: Skjenneberg and Slagsvold, 1968; Lincoln and Tyler, 1992). Thus, the growth of antlers *per se* is not a sex-limited characteristic. Nevertheless, it has been shown that the administration of testosterone to intact male reindeer induces premature maturation of the antlers and cleaning of the velvet (Ryg, 1983), as in males of other species (Goss, 1963; Bubenik, 1990), and the results of the present study demonstrate that the administration of oestradiol is similarly effective in female reindeer. This finding supports the view that, while the gonadal hormones are not essential for the development and replacement of the antlers in reindeer, they play a crucial role in synchronizing the antler cycle with the seasonal reproductive cycle (Lincoln and Tyler, 1994) and presumably dictate the dimorphism in antler size.

While the effects of sex steroids on the ossification and cleaning of the antler are well recognized, their stimulatory effects on antler growth and development are poorly described. In the present study, the antlers produced by the oestradiol-treated ovariectomized reindeer were almost twice as heavy and carried significantly more well-developed branches (points) than those produced in the years before the steroid treatment. This effect is unlikely to be due merely to the increase in age and physical size, since the ovariectomized animals were already fully physically mature before the steroid replacement was initiated, and the antlers that developed during the previous two years showed no age-dependent incremental change. The antlers produced by the ovariectomized reindeer during treatment with oestradiol were apparently physically stronger since none was broken during winter through contact with fences and during interactions with other animals, in contrast to before treatment when breakages were frequent. Overall, these observations support the view that oestradiol normally acts to promote the growth and morphological development of antlers, as well as regulating their terminal maturation. The cellular mechanisms by which sex steroids stimulate antler growth have not been investigated, but most probably

involve the induction of anabolic and proliferative effects on the bone cells and the activation of growth factors, on the basis of studies of skeletal-derived osteoblasts that express both oestrogen and androgen receptors (Barzell, 1988; Eriksen *et al.*, 1988; Colvard *et al.*, 1989). Insulin-like growth factor I (IGF-I) is one candidate regulator, since IGF-I receptors are expressed in the growing tip of the antler in red deer and IGF-I may mediate the effects of growth hormone to induce the initiation of antler growth in spring (Suttie *et al.*, 1985; Suttie and Fennessy, 1992). In osteoblasts from other species, oestradiol induces cell proliferation due, at least in part, to the local production of IGF-I and IGF binding proteins (Ernst *et al.*, 1989; Kasperk *et al.*, 1989). Thus, tissue concentrations of the growth factor within the growing antler may be modulated by the sex steroids to affect growth (Sempéré *et al.*, 1989). These observations are in agreement with the hypothesis developed from studies in male red deer (Lincoln, 1971, 1992) that proposes that low concentrations of gonadal steroids (both androgens and oestrogens) secreted during the sexually inactive phase of the seasonal reproductive cycle stimulate growth and full morphological development of the regenerating antler, while high concentrations of sex steroids produced before the mating season induce the full mineralization of the antler bone and the cleaning of the velvet to produce the hard antler.

Since increased concentrations of sex steroids are required to maintain the hard antlers (Goss, 1963), one prediction of the present study was that cessation of the treatment with oestradiol once the ovariectomized animals had hard antlers would induce casting of the antlers, as occurs in female reindeer at the time of ovariectomy (Lincoln and Tyler, 1994) and as occurs after castration in male reindeer (Hadwen and Palmer, 1922; Skjenneberg and Slagsvold, 1968) and in other species (Wislocki *et al.*, 1947; Waldo and Wislocki, 1951; Goss, 1963; Lincoln *et al.*, 1972; Sempéré *et al.*, 1989). However, removal of the oestradiol implants caused two of five animals to cast prematurely within 6 weeks, while the others cast at the normal time in spring. This ability of some individuals to retain hard antlers in the absence of gonadal steroids, as well as the ability of untreated gonadectomized

Fig. 5. Histograms showing the (a) antler weight, (b) antler points per antler, and (c) antler length in untreated ovariectomized (OVX), oestradiol-treated ovariectomized (OVX + E), and intact, non-pregnant control (Intact) reindeer. The values are means $\pm$ SEM, $n = 5$. For each parameter, groups denoted by a different letter (a,b,c) are significantly different ($P < 0.05$, ANOVA with Kruskal-Wallis test).

reindeer to clean the antlers in winter partially or completely (Tandler and Grosz, 1913; Skjenneberg and Slagsvold, 1968; Lincoln and Tyler, 1994) suggests that steroid hormones from other tissues, particularly the adrenal gland, may contribute to the regulation of the antler cycle (Bubenik *et al.*, 1987). Androstenedione is present in the circulation of ovariectomized reindeer in winter, and acute stimulation of adrenal steroidogenesis provokes an increase in both androstenedione and testosterone secretion (Lincoln and Tyler, 1994). Therefore, adrenal steroids may also influence the development and retention of the hard antlers.

The erosion surface at the base of the cast antlers from the oestradiol-treated and untreated ovariectomized reindeer

was concave, and quite distinct from the flat or convex surface of antlers from intact controls. A concave casting surface is also a feature of antlers from long-term castrated male reindeer, and in males of other species that have been induced to cast prematurely by castration (Wislocki *et al.*, 1947; Goss, 1963). Casting occurs when osteoblasts migrate to the junction between the living pedicle and the dead tissue of the hard antler, triggered by the declining steroid environment (Goss *et al.*, 1992). These cells erode the bone matrix progressively until the old antler is cast. One explanation for the shape of the erosion surface at the base of the cast antler is that the live-dead junction moves slowly down into the antler pedicle due to a process of 'die-back' and, if casting is triggered early during the hard-antler phase, erosion of the bone occurs higher into the base of the old antler to produce a concave casting surface (Lincoln, 1984). If this model is correct then the 'die-back' of the dead antler tissue must be delayed in ovariectomized and castrated reindeer since casting at the normal time in spring produces a concave base to the antler. This would be consistent with the observed delay in the overall maturation and cleaning of the antlers, compared with intact females. However, treatment with oestradiol induced normal rapid cleaning but still resulted in a casting surface similar to that of ovariectomized animals, thus the effects of sex steroids on cleaning and casting can be dissociated, and it is the presence of the steroid in the winter that determines the pattern of 'die-back' at the junction between the dead antler and the living pedicle.

In conclusion, this study provides strong experimental support for the hypothesis that oestradiol secreted by the ovary acts to induce and maintain the hard antler state in female reindeer. The effect of oestradiol is likely to be biphasic, with the steroid acting initially to stimulate growth and later to inhibit growth by terminally differentiating the antler tissues. Since the normal sequence of growth, ossification and cleaning occurred in the oestrogen-treated ovariectomized reindeer in the presence of a presumed constant blood concentration of oestradiol, a progressive change in steroid concentrations is not a prerequisite for the sequential maturation of the antler. The endocrine regulation of the antler in normal animals ensures that the antler cycle is synchronized to the seasonal reproductive cycle, and that the antlers are fully developed in autumn and winter, when females are normally pregnant, and when competition for food in deep snow can be most intense between them. The selective advantage of possessing an effective weapon used in intrasexual competition under the special conditions of the Arctic (Lincoln, 1994) provides an explanation for the evolution of antlers in female reindeer.

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