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The influence of the stag on pubertal development in the red deer hind

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Abstract

The possible influence of social factors on the timing of puberty in the hind was investigated utilizing seasonally advanced (melatonin-treated) hinds and stags. Melatonin treatment of both sexes resulted in a significant advancement in the onset of pubertal ovarian activity (26 days, $P < 0\cdot001$*) and calving (27 days,* $P < 0\cdot001$*) in the treated hinds and antler casting (25 days,* $P < 0\cdot001$*) in the treated stags. Ovarian activity and calving were not influenced by melatonin treatment of the stags alone and similarly, antler casting was not affected by melatonin treatment of the hinds alone. However, a group of hinds without stags until after the onset of the breeding season, reached puberty later (5 days,* $P < 0\cdot05$*) than hinds with stags, suggesting the presence of the male is important in determining the timing of puberty.*

Keywords: *melatonin, puberty, red deer, social interaction.*

Introduction

The red deer hind normally attains puberty during the autumn breeding season, at about 16 months of age, provided a minimum live weight of 60 to 70 kg has been attained (Hamilton and Blaxter, 1980; Kelly, Fennessy, Moore, Drew and Bray, 1987). The breeding season, or rut, is characterized by stags aggressively competing to hold harems of hinds and typically includes periods of intense roaring, herding and fighting behaviour (Clutton-Brock, Guinness and Albon, 1982).

The likely major determinant of the timing of puberty in this species, is circannual photoperiod, since modifying daily photoperiod alters the timing of puberty (Webster and Barrell, 1985). Furthermore, the strategic administration of melatonin has been shown to advance the onset of puberty in hinds, as well as to induce changes in the seasonal pattern of coat growth and live weight (Webster and Barrell, 1985; Asher, 1990; Fisher, Fennessy and Johnstone, 1990; Wilson, Walker, Bond, Middleberg and Staples, 1991; Fisher, Meikle and Fennessy, 1992; Adam, 1992; Wilson, 1992). Similarly, treatment of adult stags results in earlier rutting behaviour and changes in live weight, coat and testicular growth and antler status including casting (Lincoln, Fraser and Fletcher, 1984; Adam, Moir and Atkinson, 1986; Fisher and Fennessy, 1990; Webster, Suttie and Corson, 1991; Wilson *et al.*, 1991; Adam, 1992).

In the wild, red deer stags may become reproductively active in advance of the hinds, and this may promote the onset of the breeding season in the females (Lincoln and Guinness, 1973). Hinds thus stimulated, may further stimulate the stag and hence the rut quickly gains momentum. Exposure of farmed adult red deer hinds to normal (Moore and Cowie, 1986; McComb, 1987) or seasonally advanced (Fisher and Fennessy, 1990; Wilson, 1992) stags has been observed to advance the onset of the breeding season. These observations, along with the report that physical association between hinds during the rut resulted in more synchronous conceptions (Iason and Guinness, 1985), and synchronous calving patterns in wild and farmed deer (Lincoln and Guinness, 1973; Blaxter, Kay, Sharman,

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Cunningham, Eadie and Hamilton, 1988), suggests that the complex of social interactions and behaviour that characterize the rut is itself an important component in determining the timing of the onset of the breeding season.

The objective of the present study was to investigate how the timing of puberty in the hind might be influenced by social factors, by determining the influence of normal and seasonally advanced (melatonin-treated) stags on the timing of the onset of the breeding season and seasonal changes in live weight and coat growth, normally seen in pubertal hinds (Fisher *et al.*, 1990 and 1992).

Material and methods

The timing of puberty was monitored in 50 yearling (approx. 15 months of age in January 1990) hinds (no. = 10 per treatment) allocated to one of the following treatments, each with two replicates, for mating (i.e. five hinds and one stag per replicate): (1) hinds alone (i.e. untreated and with no stag present until after the onset of the breeding season); (2) control hinds + control stags; (3) control hinds + melatonin-treated stags; (4) melatonin-treated hinds + control stags; (5) melatonin-treated hinds + melatonin-treated stags.

Melatonin treatment in both hinds and stags (adult) involved implantation of two subcutaneous implants, each containing 18 mg melatonin (Regulin, Young's Animal Health (NZ) Ltd, Upper Hutt, NZ) on each of three occasions, 30 November, 29 December and 30 January (control hinds received no implants). All hinds (melatonin-treated and untreated) were maintained as one group during the period from the initiation of melatonin treatment until the time when stags were introduced (18 January, 1990). Treated stags were moved to separate farms, about 4 km away, from the beginning of melatonin treatment, and were kept separate until joining the hinds. Except for the group that contained hinds alone, hinds were allocated to run with one of two stags sited in adjacent paddocks (i.e. one replicate of five hinds plus one stag per paddock), from 18 January, 1990, until 19 March when replicate groups were combined and one of the stags removed. The treatment groups were separated as far as practically possible, the hinds-alone group by at least 500 m from the other treatments, which were all separated by at least 250 m. In order to assist farm management and to ensure maximum fertility by giving hinds access to more than one stag, the appropriate control and melatonin hind treatment groups were combined on 2 April with either a control or melatonin-treated stag. On 30 April, all groups were combined and stags replaced by a single novel adult stag for 25 days. The hinds-alone group was subsequently added to this mating group on 7 May.

Blood samples were collected from all hinds via jugular venipuncture whilst the animals were restrained in a compressed air operated deer crush. This was undertaken weekly from 30 November to 22 January and then twice-weekly until either 30 April (all hinds with stags) or 7 May (hinds alone group). The onset of ovarian activity, based on plasma progesterone concentrations, was taken as the first, short ovarian cycle preceding the normal cyclic pattern (Jopson, Fisher and Suttie, 1990). Plasma progesterone concentrations were determined using the direct solid-phase ^{125}I radioimmunoassay (Diagnostic Products Corporation, Los Angeles, USA) that has been validated for use in red deer (Jopson *et al.*, 1990). The inter-assay coefficients of variation (CV) were 0·120 and 0·096 for plasma pools containing 3·76 and 8·32 µg/l progesterone, respectively. The intra-assay CV, measured on 20 duplicate pairs per assay (no. = 4) was 0·087. The limit of detection of the assay, defined as the apparent concentration at two standards deviations above the zero standard, was 0·06 µg/l.

Hind live weights were recorded at about 3-week intervals from 29 November 1989 to 26 April 1990 and thereafter on 7 July, 30 August, and 2 October 1990. On each occasion that hinds were weighed or blood sampled their coat condition was subjectively assessed visually as either summer (reddish-brown), moulting or winter (greyish-brown) as reported by Ryder (1977). Calving dates of individual hinds and the date of hard antler casting in stags were monitored by daily observation. No coat observations were undertaken on the stags. Roaring was counted during 30-min observation periods between 07.00 and 10.00 h on 21 February, 28 February and 7 March.

All data are presented as means with standard errors. Comparisons between groups were examined by analysis of variance and in a 2 × 2 factorial design, plus a control (hinds alone), the factors being hinds with or without melatonin and stags with or without melatonin. Live weight on 2 October 1990 was confounded by pregnancy status, so was adjusted by using a covariate for the non-pregnant hinds.

Results

After the experiment began, it was apparent that two of the hinds (both melatonin-treated, one with a control and one with a melatonin-treated stag) were not purebred but were wapiti × red animals (Moore

Table 1 *Effect of melatonin treatment and the presence of untreated or melatonin-treated stags on ovarian activity, calving, and live-weight gain in hinds*

	Onset of ovarian activity			Calving date			Live-weight gain (kg)	
	Proportion	Mean	s.e.	Proportion	Mean	s.e.	2 Feb-26 Apr (late summer/ early autumn)	26 Apr-30 Aug (late autumn/ winter)
Hinds alone†	8/10	17 Apr	1·9 days	8/10	31 Dec	2·0 days	6·5	–2·8
Control hinds + control stags	9/10	11 Apr	1·4 days	8/10	6 Dec	2·3 days	5·8	1·7
Control hinds + melatonin stags	9/10	13 Apr	1·9 days	9/10	12 Dec	4·4 days	5·1	–0·5
Melatonin hinds + control stags	8/8	20 Mar	2·6 days	8/8	13 Nov	3·1 days	3·8	3·5
Melatonin hinds + melatonin stags	9/9	15 Mar	2·0 days	8/9	11 Nov	2·1 days	4·0	4·1
s.e.d.		2·63 days			4·03 days		0·88	1·12

† Stags were precluded from this group until 7 May, equivalent to a calving date of 25 December.

and Littlejohn, 1989) and although they remained to keep group numbers similar they have not been included in the analyses. In early February, a third animal (melatonin-treated hind running with a control stag) died from misadventure.

Ovarian activity (Table 1) in those hinds with stags commenced in mid April in untreated hinds but was significantly earlier in melatonin-treated animals (17 March (s.e. 1·7 days) *v.* 12 April (s.e. 1·2 days); $P < 0{\cdot}001$). Two control hinds, one with a control stag and one with a melatonin-treated stag, did not have plasma progesterone profiles indicative of the initiation of ovarian cyclicity, and failed to calve. There was no significant influence of melatonin treatment of stags on the onset of ovarian activity, irrespective of whether the hinds were treated or not. Neither were there any significant interactions between hind and stag treatments.

The hinds-alone group were significantly later than all other hinds and 5·4 days later ($P < 0{\cdot}05$) than the untreated hinds with stags. Two of the hinds-alone group displayed no progesterone secretion indicative of ovarian activity, yet conceived in the period after sampling had ceased, indicating that the delay in ovarian activity in this group of hinds was probably underestimated.

The mean time of calving (Table 1) reflected the time of onset of ovarian activity. Melatonin treatment of the hinds resulted in a 27-day advancement in mean calving date (12 November (s.e. 1·8 days) *v.* 9 December (s.e. 2·6 days) in untreated hinds; $P < 0{\cdot}001$), but there was neither any influence of stag treatment, nor any interaction. In the hinds-alone group (kept without a stag until after the onset of ovarian activity), 8/10 subsequently calved. Four other hinds failed to calve, two in the control hind-control stag group and one each in the control hind-melatonin stag and melatonin hind-melatonin stag groups. Of the hinds that went to the stag prior to the onset of the breeding season, 33/37 (89·2%) subsequently calved, with 31/33 (93·9%) of these conceiving at their first oestrus.

At the beginning of the experiment (29 November 1989) the hinds weighed 67·8 (s.e. 0·7) kg with no significant differences between groups. The seasonal pattern of live-weight change was advanced in melatonin-treated compared with untreated hinds (Table 1). In the late summer/autumn period, there was less weight gain (3·9 kg) in these animals than in both untreated groups of hinds whether they were running with stags (5·5 kg; $P < 0{\cdot}05$) or not (hinds alone; 6·5 kg; $P < 0{\cdot}01$). In contrast, in the late autumn/winter period there was a greater weight gain (3·8 kg *v.* 0·6 kg in untreated hinds running with stags, $P < 0{\cdot}01$; and –2·8 kg in hinds alone, $P < 0{\cdot}001$). However, eventually (2 October 1990) live weight did not differ significantly between treatment groups (89·5 (s.e. 1·1) kg). Hind live weight was not significantly influenced by whether or not the stag was treated with melatonin. The only significant ($P < 0{\cdot}05$) effect of the stag was seen in the late autumn/winter period, with the hinds-alone group losing an average of –2·8 kg, while other groups generally maintained or increased weight (average changes of –0·5 to 4·1 kg).

The timing of the summer coat moult (occurring on average on 9 March) and winter regrowth (average 11 April) in the hinds was significantly advanced by melatonin treatment of the hinds (16·4 days, $P < 0{\cdot}001$ for summer and 22·6 days, $P < 0{\cdot}001$ for winter). The absence of a stag (i.e. hinds alone) resulted in a 7·2 day ($P < 0{\cdot}01$) delay in the onset of moulting compared with untreated hinds running with stags. The delay was significant when compared with untreated hinds running with melatonin stags (9·4 days; $P < 0{\cdot}01$) but not with untreated stags (4·9 days). The only influence on the duration of the moulting period (on average 32·7 days) was a significantly ($P < 0{\cdot}05$) longer period for untreated hinds (35·9 days) compared with melatonin-treated hinds (29·6 days). Differences in coat growth were still evident during the period of winter moult/summer regrowth. On 25 September 1990, 3/10 of the hinds-alone group were moulting, 5/9 and 6/10 of the untreated hinds running with untreated or melatonin-treated stags, respectively, and 7/8 and 8/9 of the melatonin-treated hinds running with untreated and melatonin-treated stags, respectively.

Although melatonin-treated stags tended to roar more frequently than untreated animals (Table 2), there was much variation between individuals and no significant differences between groups. Melatonin treatment of the stags resulted in a significant ($P < 0{\cdot}05$) 25-day advancement in mean antler casting date (15 August (s.e. 9·2 days) *v.* 9 September (s.e. 4·0 days)), but there was no significant effect of hind treatment nor were there any interactions.

Table 2 *Individual roaring rates counted over a 30-min period, three times prior to the normal breeding season, and antler casting dates, in the two stags from each experimental group†*

	Control stags with:		Melatonin stags with:	
	Control hinds	Melatonin hinds	Control hinds	Melatonin hinds
Roars per 30 min				
21 February	0, 0	0, 45	0, 0	0, 9
28 February	0, 0	3, 125	0, 8	0, 53
7 March	0, 0	5, 110	52, 133	113, 136
Antler casting	11 and 16 Sept	4 and 5 Sept	26 and 30 Aug	20 Jul and 15 Aug

† Values recorded from each of the two stags in each treatment group.

Discussion

Farming may modify many ecological, environmental and genetic parameters with the potential to influence physiological function in deer (see Fisher and Bryant, 1993). In management systems where the timing of stag introduction, sire selection, the separation of animals by sex and age and the prevention of aggressive behaviour between stags during the rut may all be artificially modified, the potential for social cues to enhance or impair reproductive performance should be considered.

In the present study there was evidence for an effect of the presence of the stag. That is, when compared with hinds running with stags, the hinds running without stags reached puberty later, and also showed small differences in the patterns of coat growth and live-weight change (although during winter this could have been confounded by stage of pregnancy) that are indicative of delayed seasonality. Male presence can, in many species, induce or enhance complex changes in reproductive function in females (Whitten, 1956; Bronson, 1989). Amongst domestic farm animals, for example, as well as the much studied ram effect, the bull may hasten the onset of breeding activity in cattle (Macmillan, Allison and Struthers, 1979) and the boar hastens the onset of puberty in the gilt (Brooks and Cole, 1970). The mechanism for this effect in deer is largely unknown but it is likely that it is mediated via a combination of visual, olfactory, tactile and auditory cues.

Whilst the presence of a stag influenced the timing of puberty, seasonally advanced (melatonin-treated) stags had no further influence, irrespective of whether the hinds were untreated, or seasonally advanced with melatonin. This result is in contrast to our previous report where seasonally advanced stags stimulated earlier breeding activity in both control and melatonin-treated adult hinds (Fisher and Fennessy, 1990). There are several possible reasons for this difference. It may indicate an effect of age or reproductive experience with pubertal hinds being naïve and unable to respond. This possibility is supported by the later calving dates normally noted in first calving hinds (Bray and Kelly, 1979) and by the report of significant variation in pre-ovulatory events in pubertal compared with adult hinds (Argo and Loudon, 1992). Secondly, in the present experiment treatment combinations were maintained separately with wide physical separation between groups whereas in the earlier study, untreated and melatonin-treated hinds were kept together, in the presence of either untreated or melatonin-treated stags. Thus, any social effects of a seasonally advanced stag might require the presence also of seasonally advanced hinds as noted by Fisher, Fennessy and Milne (1988). Moreover the presence of oestrous (progestagen-PMSG treated) ewes increased the efficacy of rams in inducing oestrus and ovulation in progestagen-treated anoestrous ewes (Knight, 1985). Thirdly, stags and hinds were joined on different calendar dates in our pubertal study (18

January), compared with the earlier adult study (3 March). It has been demonstrated that the timing of ram introduction is a major factor in determining the oestrous and ovulatory responses of anoestrous ewes (Edgar and Bilkey, 1963; Hall, Fogarty and Gilmour, 1986; Scott and Johnstone, 1994), thus the stag may be more effective when introduced at certain times, perhaps nearer the breeding season. However, an inductive, synchronous 'stag effect', similar to the ram effect (Underwood, Shier and Davenport, 1944; Martin, Oldham, Cognie and Pearce, 1986) has not yet been demonstrated. Fourthly, perhaps interactions between seasonally advanced animals are more evident when melatonin treatments result in modest advances in reproductive activity. A large or maximal advance due to melatonin treatment might have precluded the additive effects of interactions between hinds and stags. Finally, there are inherent difficulties associated with these types of experiment. It is difficult to isolate completely (particularly from auditory and olfactory stimuli) groups of animals on a single farm. There is wide variation in rutting behaviour between individual stags and the relatively low numbers of stags used (no. = 2 per group), would exacerbate this problem. Another unknown factor is the importance of opportunity for aggressive competition between males.

Notwithstanding all of these points, there is some evidence, both for and against a social facilatory effect on puberty in red hinds. Blaxter *et al.* (1988) reported that the presence of older companion hinds at mating did not influence the time of calving in younger hinds. In contrast, others have indicated that, in field studies, some groups of untreated pubertal hinds run with melatonin or progesterone-PMSG treated animals at mating, calved earlier or more synchronously than expected (Wilson *et al.*, 1991).

In conclusion, social factors may influence the timing of the breeding season in pubertal hinds but these effects appear to be relatively modest.

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