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Voluntary intake, testis development and antler growth patterns of male red deer under a manipulated photoperiod

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ABSTRACT

Six young red deer stags were placed on a photoperiod of 5 alternating periods of 2 months of 16 hours light: 8 hours dark each day (16 L:8 D) followed by 2 months of 8 L:16 D for 20 months. Food intake, whether the antlers were present, and if present, whether growing, cleaning or hard and testis diameter were recorded. Each stag showed 5 peaks and 5 troughs of food intake in response to the manipulated photoperiod. There were 4 cycles of gonadal development and regression as the testes did not descend from the inguinal canal during Period 1; testes grew in short day periods and diminished in size in long day periods. There were 4 cycles of antler growth and casting; antler cleaning occurred on short days and casting on long days. Male red deer are capable of responding to a square wave daylength pattern as a sinusoidal pattern.

Keywords Red deer; square wave pattern; photoperiod; antler; food intake; testis

INTRODUCTION

Male deer show marked annual rhythms of growth (Blaxter *et al.*, 1974; Fennessy *et al.*, 1981; Suttie *et al.*, 1983), voluntary food intake (Blaxter *et al.*, 1974; Suttie *et al.*, 1983), gonadal development (Lincoln, 1971) and antler growth (Jaczewski, 1954; Goss, 1969; Suttie and Kay, 1982). Deer are capable of growing up to 4 sets of antlers each year when the frequency of the sinusoidal photoperiod is increased to 4 per year (Goss, 1969). In addition 2 cycles of growth, food intake and gonadal development have been recorded in response to a doubled photoperiodic frequency in one year in penned red deer (Simpson *et al.*, 1984). Male sheep are capable of responding to alternating periods of long (16 h light:8 h dark) and short days (8 L:16 D) as annual cycles as evidenced by cycles of gonadal development and regression (Lincoln and Davidson, 1977).

The present study was designed to determine the response of male red deer in terms of food intake, antler and testis growth to 3 cycles of photoperiod within 1 calendar year where the change in photoperiod was imposed as a square wave pattern. A square wave pattern was used so that daylength change and antler cleaning and casting could be precisely related, because a sinusoidal waveform cannot permit the establishment of a cause-effect relationship between a daylength change and a physiological effect.

MATERIALS AND METHODS

Six male red deer calves (born December 1981) were placed in individual pens in a light controlled room on 7 March 1982. The deer were subjected to a manipulated photoperiod of 16 L:8 D for 2 months alternating with 2 months of 8 L:16 D for a period of 20 months. The deer were fed a high quality pelleted diet consisting of 55% barley 35% lucerne and 10% linseed oilcake with added minerals and vitamins to appetite (Fennessy *et al.*, 1980). Food intake and whether the antlers were present or absent and if present whether growing in velvet, cleaning in hard antler or cast were recorded every 2 to 3 days. One, 4 and 7 weeks after each light change the deer were immobilised with 100 mg xylazine (Rompun, Bayer Ltd) administered via a syringe projectile (Corson *et al.*, 1984) and testis diameter and antler length measured. Antlers were removed after cleaning 2 cm above the antler-pedicle junction (leaving a stub) and weighed.

Biometric Analysis

A sine wave plus trend equation was fitted to the food intake data for each stag and for the pooled data by non linear least squares. The model equation is given by:

$$y = a + ct + b \sin [2 (t - 0)/w]$$

where y is food consumption (kg)
t is time (weeks)
$a + ct$ is a linear trend representing growth
$w = 17.6$ weeks is the period
0 and b are the phase and amplitude of the sine curve.

The estimated parameter values for the pooled data ($\pm$s.e. in parentheses) were:
$0 = 1.76$ (± 0.24)
$b = 2.77$ (± 0.24)

c = 0.067 (±0.008)
a = 10.12 (±0.47)

Chi square goodness of fit tests were used to analyse data from the present study on a manipulated photoperiod in relation to data from a natural photoperiod.

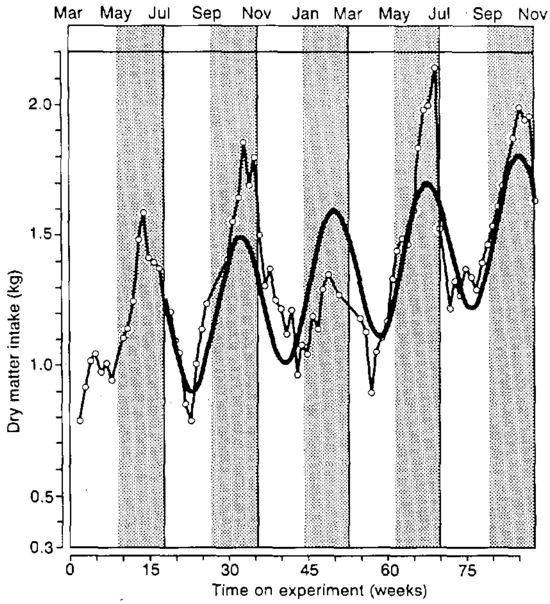

FIG. 1 Food intake (g/week; mean ± sem) of 6 stags. The hatched areas represent periods of short days (8 L:16 D) and the adjacent clear areas long days (16 L:8 D). The sine wave fitted to the data is superimposed.

RESULTS

In response to the periods of alternating long and short days, 5 peaks of food intake occurred (Fig. 1). Minimum food intake corresponded with long days and maximum food intakes (peaks) corresponded with short days. The minimum of food intake was 93 d ± 7.7 (mean ± sem) after a change from long to short daylength similar to the 102 days from the summer solstice in conditions of natural photoperiod (Fennessy 1981 and unpublished data). Conversely on a natural photoperiod deer reached peak food intake 157 days after the shortest date (winter solstice) whereas on the manipulated photoperiod the time was 99 ± 0.4 d from short to long daylength ($P < 0.02$).

In response to the changes in daylength there were 4 periods of testis growth followed by regression (Fig. 2). Testis growth occurred during short days and regression commenced sometime between 1 to 4 weeks after a change to long days. Similarly testis growth began sometime between 1 to 4 weeks after a change from long to short days.

In Tables 1 and 2 the antler grown from May at the start of the study until November and cast about

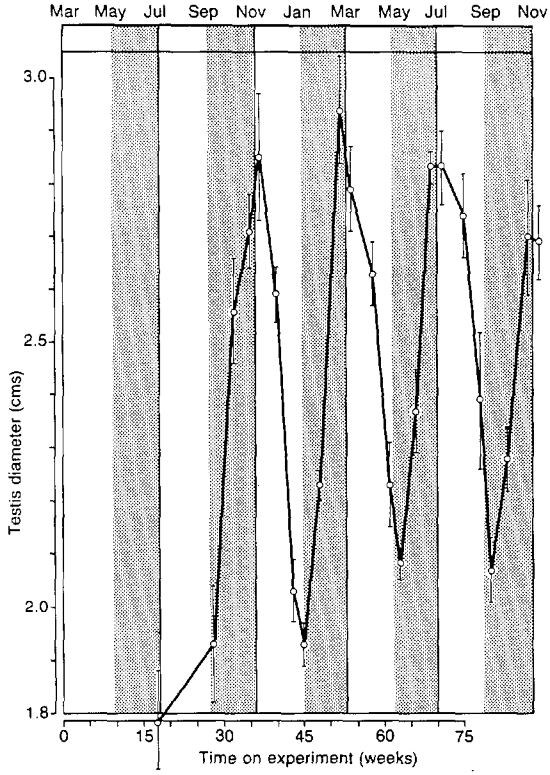

FIG. 2 Testis diameter (cm, mean ± sem) of 6 stags.

January is referred to as Antler 1. Subsequent antlers grown from January-March, May-July and September-November are referred to as Antlers 2, 3 and 4 respectively. In the tables Antler 1a refers to

TABLE 1 Period (days) from a change from long to short days to antler cleaning.

Antler Growth Period	Median	Range	n
1a	67	-	1
1	55	54-59	6
2	56	54-64	6
3	56	52-60	5
4	55	52-63	6

TABLE 2 Period (days) from a change from short to long days to antler casting.

Antler Growth Period	Median	Range	n
1a	67	-	1
1	46	36-65	6
2	55	46-60	5
3	56	51-75	6
4	46	41-51	6

TABLE 3 Combined antler weight (g). Only 5 stags grew antler 3 as one stag failed to cast his second antler.

		Antler Growth Period			
		1	2	3	4
Mean	67	184	458	460	504
sem	-	28	80	92	116
n	1	6	6	5	6

the precocious stag who grew his first antler from May-July at the start of the study.

The majority of stags grew their antlers during each period of short days after the first cycle. However 1 stag grew antlers each cycle, i.e., 5 antlers during the study, while 1 stag failed to cast his second antler and thus failed to grow antler 3 although he cast at the next appropriate photoperiod change and regrew normally (Fig. 3). Antler cleaning (defined as the first day cleaning was observed) occurred on short day periods 55 days after the light change from long to short daylength (Table 1). Conversely antler casting occurred on long day periods 46 to 56 days after the light change from short to long daylength (Table 2). The antler weight increased after the first antler but thereafter remained similar (Table 3). The first antler grew at 0.45 cm ± 0.06/d (mean ± sem, n = 6) for 71 ± 6.3 d from antler initiation to cleaning while subsequent antlers grew at 0.52 ± 0.02 cm/d for 62 ± 1.9 d (n = 16).

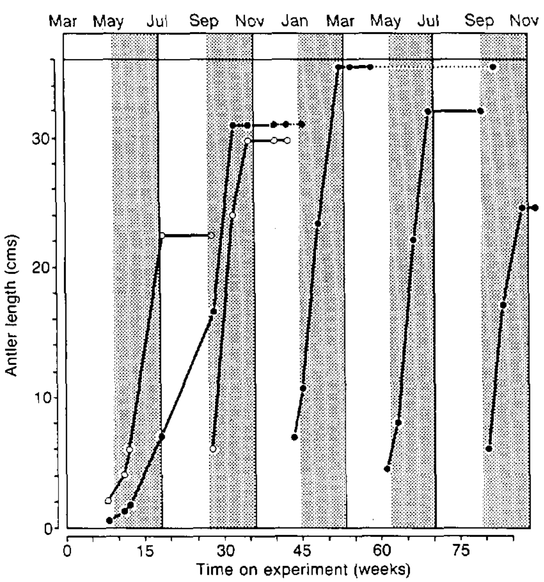

FIG. 3 Antler length (cm, mean) of 6 stags. The open symbol indicates a precocious stag who grew a set of antlers during each period of the study. A broken line indicates that although some individuals had commenced antler casting some had not.

DISCUSSION

Male red deer are capable of responding to light in a square wave pattern as they do to an annual cycle and the imposition of 3 such patterns in 1 calendar year elicited 3 cycles of food intake, gonadal development and regression and antler growth. There was a lag in response time between a light change and the onset of change between increasing and decreasing food intake. For example the peak food intake occurred towards the end of short-day periods whereas under the natural photoperiod it would have been expected to occur during increasing days (Simpson *et al.*, 1984). However of the 2 components of the lag i.e., time to reach peak food intake and time to reach minimum food intake, only 1 was significantly different from the natural photoperiod, namely the former. Possibly the observed annual pattern is a combination of 2 cycles, namely one directly mediated by photoperiod and the other by sex hormones, especially testosterone.

Stags of the same age as those in the present study fed indoors a similar ration but maintained on a natural photoperiod ate 2.3 to 4 kg dry matter/d at peak food intake and 0.5 to 1.3 kg/d at minimum food intake (Suttie *et al.*, 1983). In contrast the stags in the present study ate 1.6 to 2.1 kg/d at peak food intake but 0.8 to 1.2 kg/d at minimum food intake. Thus as cycle frequency has increased, amplitude has decreased but this seems mainly due to smaller peak food intakes and similar minimum food intakes.

The sine wave fits the data well except for the peak during January-March, when intake is much lower than either the previous or following peaks. The stags reached minimum food intake late during the previous period of long days and they may have had insufficient time to reach the maximum possible food intake before the influence of short days (non-stimulatory for food intake) caused a further loss of appetite.

Lincoln and Davidson (1977) found that Soay rams took 2 to 5 weeks to begin testis growth after exposure to short days. This agrees well with the present study where it took 1 to 4 weeks to detect a measurable change in testis size. There was no indication of deer becoming refractory to stimulatory photoperiods as suggested by Lincoln and Davidson, (1977) possibly because in the present study the cycles alternated too quickly.

Clearly short day length is stimulatory for testis development and *vice versa*. However peak and minimum testes diameter reported by Suttie (1981) were about 3 cm and 1.5 cm respectively in stags of the same age compared with about 2.8 cm and 2.1 cm (Fig. 3) as in the present study. Thus the testes of stags on the manipulated photoperiod neither grew as large or regressed as much as stags on natural photoperiod.

Deer cleaned and cast their antlers in response to short and long days respectively. The precocious stag who grew, cleaned and cast antlers before his fellows had completed the growth of their first set is of some interest. Although it was not possible to weigh the stags in this study, the precocious stag was clearly the largest at this time. Suttie and Kay, (1982) developed a theory that the growth of the first antler is determined more by the body size of the stag than the photoperiod. The precocious stag provides further evidence for this theory as he grew his antler during short day length which in older stags is inhibitory for antler growth. In the present study, although antler growth occurred in the majority of animals during short-day-length periods, antler casting followed by initiation of growth always occurred during long-day-length periods. The antlers were much smaller than those recorded in similar deer elsewhere (Suttie and Kay, 1982) probably partly due to the fact that the deer had only about half the normal time to grow their antlers. The fact that the antlers stopped growing before they reached their full size shows that either some inhibitory factor stopped their growth or some stimulatory factor was withdrawn. It is considered that testosterone secreted in response to the short day-length period inhibited antler growth (Suttie *et al.*, 1984).

The aim of this study was to determine whether deer could respond to day length of a square wave pattern; this they clearly can and also they clean and cast their antlers at approximately the same time in relation to the manipulated photoperiod. It is felt that the manipulated photoperiod can be used with a degree of confidence in future studies relating to the exact mechanism of antler casting.

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