

Photoperiodic requirements for rapid growth in young male red deer

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Abstract

Winter growth of young male red deer can be increased by exposure to 16 h of light (L) and 8 h of dark (D) per day (16L : 8D). This study tested the duration of photoperiod required for this growth response, determined if the time to reach slaughter weight can be reduced and monitored plasma IGF-1, prolactin and reproductive development. Fifty male calves were allocated to five equal groups. Four groups were housed indoors and for 33 weeks from the winter solstice (22 June, southern hemisphere) until 11 February were placed under either 16L : 8D (16L), 13·25L : 10·75D (13L), 10·75L : 13·25D (11L) or 8L : 16D (8L) photoperiods. The fifth group of deer (OC) remained outside in a gravelled enclosure. All groups were given a pelleted diet ad libitum. Group food intake was recorded daily, individual live weight was measured weekly and testes diameter and blood samples taken at weekly or 2-week intervals.

Plasma prolactin concentrations in 16L increased within 4 weeks of treatment and were different ($P < 0.001$) between groups from 14 August to 4 September. IGF-1 increased in both 16L and 13L 4 weeks after treatments and then increased further in 16L above that of 13L ($P < 0.01$). All groups grew at the same rate for the first 7 weeks. 16L then gained more weight ($P < 0.001$) than the other groups over the next 19 weeks (50.7 kg v. 38.5 for 13L, 35.7 for 11L, 37.0 for 8L and 37.4 for OC; s.e.d. 3.76). Food intake was positively related to growth rate in a similar way among the inside groups ($P < 0.001$), however there was a higher energy requirement outdoors ($P < 0.05$). A target live weight for slaughter of 95 kg was reached 7 weeks earlier for 16L than the other groups ($P < 0.01$). Testes diameter of 16L was larger than in the other groups from 13 November until 24 December ($P < 0.001$). The growth of 16L slowed from 1 January while that of OC increased and the live weight of OC was equal to 16L by the end of the experiment. OC also had the largest testes diameter from 5 February onwards ($P < 0.01$). The live-weight increase in OC was associated with increases in both prolactin and IGF-1 levels.

This study confirmed that 16L : 8D stimulates rapid growth of young male red deer during winter for sufficient time to achieve an earlier slaughter date. The live-weight advantage was lost by late summer however. The increased growth rate was mediated by food intake and associated with increases in IGF-1 and prolactin and earlier reproductive development. Photoperiods of 13 h of light per day or less did not stimulate growth and increases in IGF-1 and prolactin were of a lower amplitude than under 16L : 8D.

Keywords: growth rate, photoperiod, prolactin, red deer, somatomedin.

Introduction

Growth rate in male red deer is seasonal. Rapid growth takes place during spring and slow growth during winter, even when animals are given a high quality diet *ad libitum* indoors (Fennessy, 1982). The seasonal cycles of growth and food intake can be manipulated by photoperiod (Kay, 1979; Simpson *et al.*, 1983/84; Suttie *et al.*, 1984; Suttie and Simpson, 1985). This has led to the use of a photoperiod comprising 16 h of light (L) and 8 h of dark (D) per

day (16L : 8D) as a practical method of stimulating an early resumption of rapid growth when applied to young male red deer calves in the autumn (Davies *et al.*, 1995; Webster *et al.*, 1997a). We sought to investigate this response further as it offers potential to achieve more flexible venison production by reducing the time to reach slaughter weight. The 16L : 8D photoperiod was previously chosen by us (Webster *et al.*, 1997a), primarily because it is similar to that of the summer solstice at the latitude of our

studies (45°S) and therefore it mimics the maximum natural photoperiod during spring and summer when rapid growth occurs. However two factors suggest that 16 h light per day may not be required to initiate the growth response. First, rapid growth has normally commenced by the beginning of September when the natural photoperiod is around 11L:13D. Secondly, in our previous experiment (Webster *et al.*, 1997a) an increase in photoperiod during autumn of around 5 h of light per day to 16L:8D stimulated rapid growth, leaving open the question of whether it was the size of the increase in photoperiod or the 16 h light that were critical to the response.

The aim of the present study was a more detailed investigation of the photoperiodic requirements for stimulating growth, by exposing deer to a range of different photoperiods from 8L:16D to 16L:8D beginning on the winter solstice. Further, in our previous experiment (Webster *et al.*, 1997a) we measured the growth response to 16L:8D for a period of 23 weeks and this experiment ended while the live weight of animals exposed to 16L:8D still appeared to be diverging from control animals. However, the animals in this earlier study had not yet reached an acceptable slaughter weight so the predicted advancement of slaughter date of around 7 weeks could only be made by extrapolation of growth rates. In the present experiment we extended the period of exposure to the photoperiods to determine the actual advancement of slaughter date and to test the hypothesis that the live weight of control animals would eventually catch up to those under 16L:8D. A final component of the experiment was to determine the effects of the photoperiod treatments on plasma IGF-1 and prolactin levels, which have been implicated in the control of growth and food intake (Suttie *et al.*, 1991a; Curlewis *et al.*, 1988) and testes size, a monitor of the seasonal stage of the reproductive axis (Lincoln, 1971).

Material and methods

Experimental design

Fifty male red deer calves aged approximately 8 months (mean live weight 52.3 (s.e. 5.8) kg) were randomly allocated to five groups (no. = 10). Four groups were housed indoors on a deep litter of sawdust in separate light-proof pens which measured 7.5 m by 4.5 m, with overhead lighting designed to produce >300 lux 1 m from the ground and electric fans for ventilation. The fifth group of deer (OC) remained outside in a gravelled enclosure (25 m × 15 m). All groups were offered *ad libitum* an identical barley-based, pelleted diet containing 160 g protein per kg and 11.0 MJ metabolizable energy per kg dry matter (DM). A small amount of lucerne hay

(approx. 100 to 200 g per animal per day) was included in the diet of each group to aid rumination and reduce coat chewing. Fresh water was available at all times.

Beginning on the winter solstice (22 June, southern hemisphere) the four indoor groups were exposed to different durations of light each day, designed evenly to span the range of light between the summer (16 h of light) and winter (8 h of light) solstices. Thus, group 16L was placed under a summer solstice photoperiod (16L:8D), group 13L was placed under 13:25L:10:75D, group 11L under 10:75L:13:25D and group 8L remained on the prevailing photoperiod (8L:16D). The light treatments were applied for 33 weeks until the end of the experiment on 11 February.

Measurements

All animals were weighed weekly and food intake of each group was recorded daily. Daily food refusals were maintained at proportionately about 0.1 of food offered. The diameter of the testes was measured with vernier callipers at 2-week intervals. Blood samples (10 ml into a heparinized vacutainer) were taken in the morning at 2-week intervals except for weeks 4 to 10 after the start of treatments when weekly samples were taken.

Assays

IGF-1 was extracted from plasma following the method of Moore and Mylek (1993) and assayed by double-antibody RIA (Webster *et al.*, 1996) in four assays. The intra-assay/inter-assay coefficients of variation of red deer plasma control pools were 0.100/0.262, 0.057/0.156 and 0.055/0.138 at 206, 476 and 885 µg/l respectively. Assay sensitivity averaged 31.6 µg/l. Note: mean IGF-1 concentrations were always higher than that of the lowest control pool.

Plasma prolactin concentrations were measured in duplicate using a 4-day competition RIA with rabbit anti-cervine prolactin antiserum raised at Invermay (Asher *et al.*, 1997). Cervine prolactin antigen was iodinated using chloramine-T as described by Hunter and Greenwood (1962). Serial dilutions of plasma containing a high concentration of prolactin were parallel to the standard curve. Cross-reactivities with ovine LH, FSH and cervine GH were all less than 0.04% and with ovine prolactin 77.2%. The assay sensitivity was 3.1 µg/l and the intra/interassay coefficients of variation (two assays) for plasma containing 10.4, 33.9 and 92.2 µg/l were 0.037/0.042, 0.039/0.054 and 0.041/0.058 respectively.

Data analysis

Live weights for each week and the changes in live weight over specific periods were analysed by

ANOVA, assuming independence of individuals within group and fitting treatment with a covariate adjustment for the previous 3 weeks live weight for each animal. This was based on testing the order of antedependence (Kenward, 1987). The time to reach 95 kg live weight was analysed by ANOVA fitting treatment, with estimated values used for animals which failed to reach 95 kg by the end of the experiment based on a method for censored observations (Taylor, 1973). The regression relationship between weekly change in live weight and (DM) intake was analysed using transfer function methods with a first-order autoregressive model for errors (Box and Jenkins, 1970). Testes diameter was analysed by ANOVA, as for live weight. Peak testes diameter of each group was calculated from the maximum diameter that the individual animals attained. IGF-1 and prolactin (at sample times and meaned for individuals over relevant periods) were analysed by ANOVA on normal and log-transformed data, respectively, fitting treatment. Back-transformed means from a log analysis are significantly different when their ratio is greater than the square of the standard error of ratio (s.e.r.).

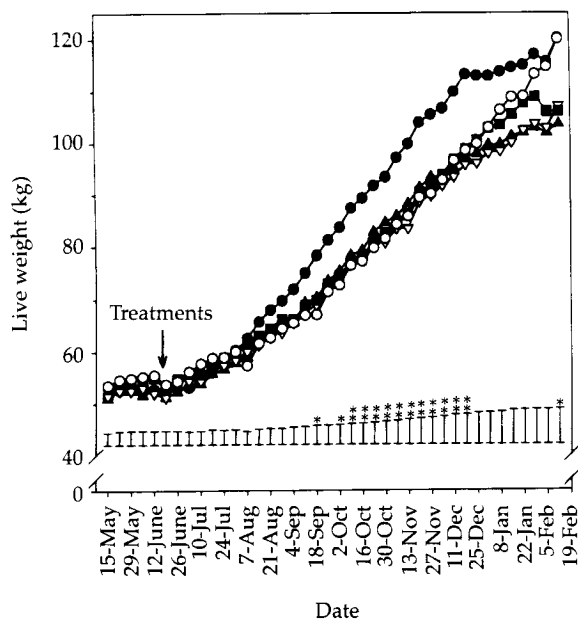


Figure 1 Mean live weights of groups (no. = 10) of male red deer maintained inside under 16L:8D (●), 13L:25L (▲), 10L:75L (▽), 8L:16D (■) or outside under a natural photoperiod (○) for 33 weeks from 22 June (winter solstice) until 11 February. The pooled s.e.d. is shown by the vertical bars at the bottom of the graph and significance level for the difference between the groups on each occasion illustrated by asterisks.

Results

Live weight

There was no difference in live weight (Figure 1) between the groups at the start of the experiment nor for the first 7 weeks after treatments commenced ($P > 0.05$). The growth rate for all groups over this period averaged 173 (s.e. 9.1) g/day. After this date (7 August) antedependence analysis revealed a significant change in the relationships between the groups ($P < 0.001$) corresponding to a sudden increase in the mean live weight of 16L which diverged from that of the other groups and was significantly greater by 18 September. 16L animals gained more weight ($P < 0.001$) than animals in the other groups from 7 August until 18 December (50.7 kg *v.* 38.5 for 13L, 35.7 for 11L, 37.0 for 8L and 37.4 for OC; s.e.d. 3.76). The growth rates over this period averaged 382 (s.e. 18.5) g/day for 16L and 279 (s.e. 9.8) g/day for the other groups. The mean date at which an acceptable target live weight for slaughter of 95 kg was reached was 7 weeks earlier ($P < 0.01$) for 16L than for the other groups (6 November *v.* 26 December for other groups; s.e.d. 2.4 weeks). After 1 January the growth rate of 16L slowed noticeably and from 8 January until the end of the experiment the live weight of OC animals diverged from that of 13L, 11L and 8L groups ($P < 0.01$ from antedependence analysis) to equal that of 16L animals by the end of the experiment. Over this last 8-week period, OC gained more weight ($P < 0.001$) than the other groups (21.6 kg *v.* 7.0 for 16L, 6.4 for 13L, 11.5 for 11L and 7.3 for 8L, s.e.d. 2.4 kg).

Food intake

The DM intake of all groups increased during spring followed by a gradual decline in all groups except OC (Figure 2), although the nature of the group food intake data prevented a direct statistical comparison. The regression of daily live-weight gain *v.* food intake was given by:

$$\text{LWG (g/day)} = 181 \text{ (s.e. 22.6)} \times \text{DM intake (kg)} \\ - 117 \text{ (inside)} \\ - 217 \text{ (outside)}$$

(s.e.d. 27.3 with residual autoregression parameter of -0.42).

There was a positive slope ($P < 0.001$) with a common intercept ($P > 0.05$) for all indoor groups, together with a difference in intercept ($P < 0.05$) but not in slope ($P > 0.05$) between the inside groups and the outside group.

Testes diameter

The mean testes diameters of the groups (Figure 3) were not different ($P > 0.05$) until 16 October when antedependence analysis detected a significant

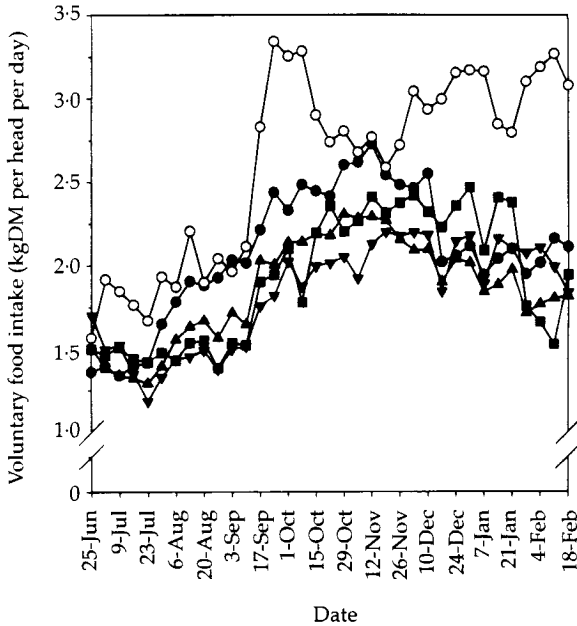


Figure 2 Mean *ad libitum* group (no. = 10) food intake (expressed as kg of dry matter per head per day) measured daily and accumulated into weekly sums, of male red deer maintained inside under 16L : 8D (●), 13-25L : 10-75D (▲), 10-75L : 13-25D (▼), 8L : 16D (■) or outside under a natural photoperiod (○) for 33 weeks from 22 June (winter solstice) until 11 February.

increase in testes diameter in 16L ($P < 0.001$). Another change was detected on 13 November as the testes diameter of OC declined slightly. From this date until 24 December there was a significant difference between the groups ($P < 0.001$) with 16L having the largest diameter. A final change ($P < 0.001$) between the groups occurred on 8 January as the testes diameter of 16L began to fall while that of OC began to increase rapidly and the latter group had the largest testes diameter from 5 February onwards ($P < 0.01$). Peak testes diameter ($P < 0.01$) and the time of the peak ($P < 0.001$) differed between treatments with a trend for larger testes in 16L and OC than in 13L, 11L and 8L groups and for the peak to occur later with decreasing photoperiod (Table 1).

Prolactin

Plasma prolactin concentrations of the 16L group increased within 4 weeks of treatment (Figure 4) and rose to a peak for all groups between 14 August and 4 September, with substantially higher mean levels over this period for 16L ($38.3 \mu\text{g/l}$) than for the other groups ($14.0, 7.3, 4.5$ and $5.9 \mu\text{g/l}$ for 13L, 11L, 8L and OC respectively; s.e.r. 1.57; $P < 0.001$). Prolactin

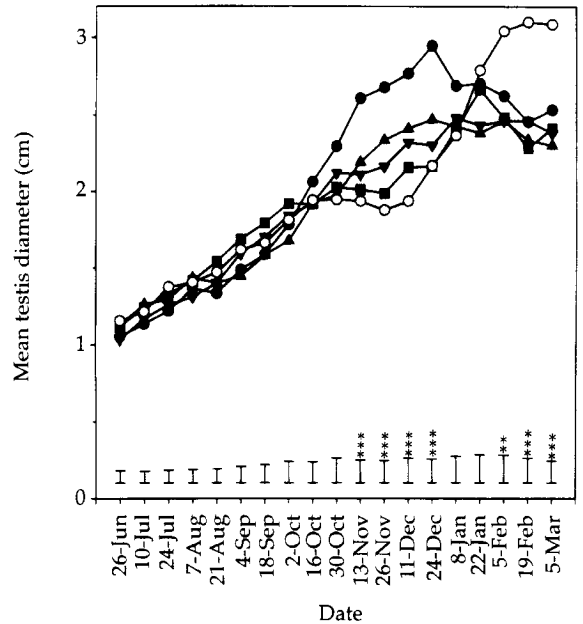


Figure 3 Mean testes diameter of groups (no. = 10) of male red deer maintained inside under 16L : 8D (●), 13-25L : 10-75D (▲), 10-75L : 13-25D (▼), 8L : 16D (■) or outside under a natural photoperiod (○) for 33 weeks from 22 June (winter solstice) until 11 February. The pooled s.e.d. is shown by the vertical bars at the bottom of the graph and significance level for the difference between the groups on each occasion illustrated by asterisks.

levels of 13L also increased and were greater ($P < 0.05$) than those of OC during this period. Prolactin levels in the OC group increased from 30 October, and there was a significant ($P < 0.001$) difference between the groups (13.7, 8.8, 5.4, 15.1 and $36.6 \mu\text{g/l}$; s.e.r. 1.55) in the mean concentration during December. Prolactin levels of 8L animals also increased during this period but levels were lower than for the OC group ($P < 0.05$). When comparing prolactin between the two periods, August *v.* December, 16L ($P < 0.001$) and 13L ($P < 0.05$)

Table 1 Mean peak testes diameter and the mean time of the peak diameter in groups of male red deer kept indoors under various photoperiods (16L, 13L, 11L and 8L) or outdoors (OC) from the winter solstice (22 June)

Group	Peak testes diameter (cm)	Time of peak diameter
16L	3.02	22 December
13L	2.61	9 January
11L	2.59	21 January
8L	2.75	5 February
OC	3.20	19 February
s.e.d.	0.169	1.4 days

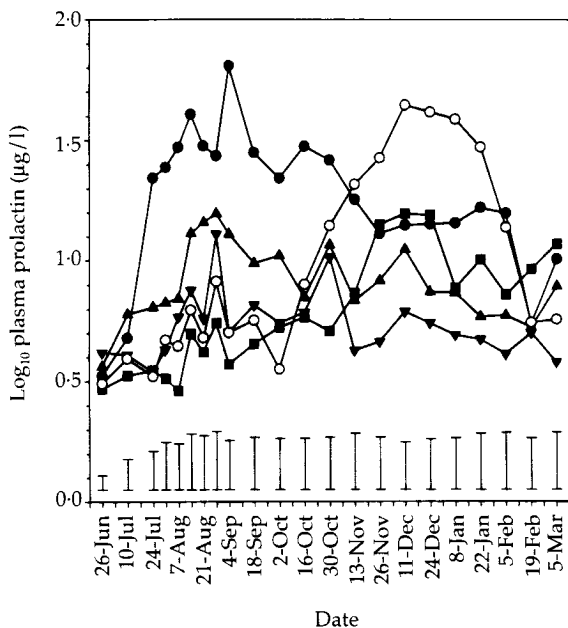


Figure 4 Mean \log_{10} plasma prolactin concentration ($\mu\text{g/l}$) of groups (no. = 10) of male red deer maintained inside under 16L:8D (●), 13-25L:10-75D (▲), 10-75L:13-25D (▼), 8L:16D (■) or outside under a natural photoperiod (○) for 33 weeks from 22 June (winter solstice) until 11 February. The pooled s.e.d. is shown by the vertical bars at the bottom of the graph. No treatment effects at individual times were significant ($P > 0.05$).

underwent decreases and 8L and OC increases ($P < 0.001$) though that of 8L was less than that of OC ($P < 0.05$).

IGF-1

There was a difference in plasma levels of IGF-1 between groups by 17 July ($P < 0.05$), around 4 weeks after treatments commenced (Figure 5). At this time IGF-1 levels of both 16L and 13L groups increased rapidly and diverged from the other groups ($P < 0.001$). Another change occurred around 6 to 7 weeks later when the IGF-1 level of 16L group increased above that of the 13L group ($P < 0.01$). IGF-1 levels in the three remaining groups began to separate from 23 October as OC and 8L increased above 11L and then 1 week later OC increased still further above 8L. IGF-1 levels of all groups peaked around the end of December or early January and then began to decline.

Discussion

This study has shown that exposing young male deer to 16 h of light per day from the winter solstice resulted in an earlier increase in growth than under natural photoperiod, resulting in animals reaching

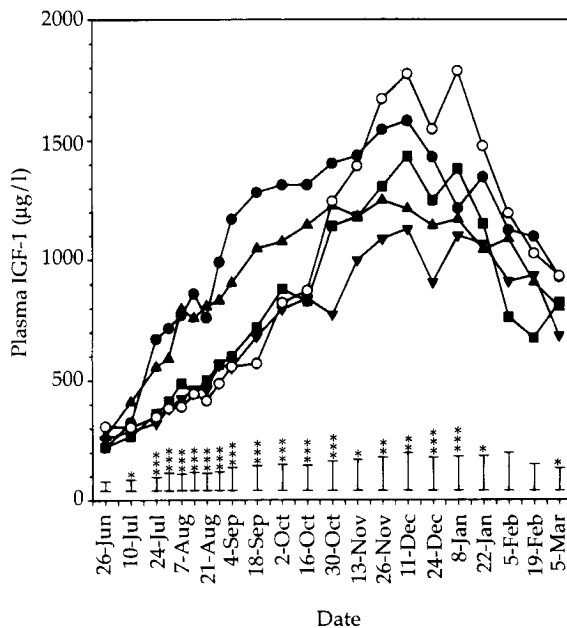


Figure 5 Mean plasma IGF-1 concentration ($\mu\text{g/l}$) of groups (no. = 10) of male red deer maintained inside under 16L:8D (●), 13-25L:10-75D (▲), 10-75L:13-25D (▼), 8L:16D (■) or outside under a natural photoperiod (○) for 33 weeks from 22 June (winter solstice) until 11 February. The pooled s.e.d. is shown by the vertical bars at the bottom of the graph and significance level for the difference between the groups on each occasion illustrated by asterisks.

slaughter weight 7 weeks earlier. In contrast, exposure to 13 h and 11 h light per day was insufficient to induce this response and growth was little different than in those animals held on a winter solstice photoperiod. Blood sampling revealed that the earlier growth in 16L compared with OC was associated with earlier increases in plasma IGF-1 and prolactin and that these increases were reduced or absent under 13L, 11L or 8L. It should be noted that the blood sampling regime used in this study cannot illustrate detailed secretory activity of the hormones measured. However, our sampling should accurately reflect the long term changes in hormone levels, as there is no evidence of circadian variation of these hormones in deer (Bubenik *et al.*, 1983) and in addition to help minimize any circadian variation we took each sample at a similar time of day. Measurement of testes diameter suggested that the seasonal reproductive cycle was also advanced by 16L:8D.

The 16L:8D photoperiod successfully advanced rapid growth and confirmed the usefulness of this technique as a practical method to advance slaughter date of young male deer as has been suggested

previously (Davies *et al.*, 1995; Webster *et al.*, 1997a). In contrast, photoperiods comprising 13 h light or less were insufficient to cause the early growth response, reinforcing the importance of using 16L:8D. This experiment has extended our knowledge of this response by demonstrating that increases in IGF-1 and prolactin precede the growth response under 16L. Lower amplitude increases in these hormones were associated with the absence of rapid growth in 13L indicating the importance of these hormones for this growth response. A marked increase in IGF-1 coinciding with spring increases in appetite and growth has been shown previously in male red deer (Suttie *et al.*, 1989; Suttie *et al.*, 1991a; Adam *et al.*, 1996) and both IGF-1 and growth increased under 16L:8D in reindeer (Suttie *et al.*, 1991b; Suttie *et al.*, 1993). Nutritional state is a potent regulator of IGF-1 levels in red deer (Webster *et al.*, 1996) indicating that the increase in IGF-1 may be a consequence of the seasonal increase in food intake rather than a cause but this does not preclude a driving effect of IGF-1 on appetite. In the present study IGF-1 appeared to precede the increase in food intake suggesting that this latter mechanism may also be present. A seasonal cycle of prolactin secretion which is related to the photoperiod cycle in red deer has been known for some time (Brown *et al.*, 1979) and evidence suggests that unlike IGF-1 this cycle is not a result of changes in food intake (Suttie and Kay, 1985). There is evidence that prolactin may be involved in the regulation of food intake in deer (Curlewis *et al.*, 1988; Milne *et al.*, 1990; Ryg and Jacobsen, 1982; Suttie and Corson, 1991) but a clear rôle is not yet established.

The regression of live-weight gain on DM intake indicated first that the benefits of 16L:8D in promoting growth are mediated by increased food intake and secondly that there was a higher energy requirement for animals outdoors. This is further evidence that exposure to 16L:8D during winter is advancing the normal phase of rapid growth and high food intake which occurs during spring. When using this technique for practical purposes, important points to be borne in mind are that increased food demands of the growing animals during winter must be met and that there is no long term live weight advantage, only earlier dates that certain live weights are reached. The higher energy requirement outdoors is presumably due to greater heat loss of these animals. In previous studies at Invermay this difference has not been significant (Webster *et al.*, 1997a and b) indicating that housing may reduce food costs in certain years. One possible reason for this is variations in climate but the lack of detailed climatic records and different experimental periods make comparisons between years difficult.

In a previous study in which 16L:8D was used to initiate rapid growth, it was proposed that because of evidence supporting endogenous rhythmicity of appetite and growth cycles in deer (Loudon, 1994; Loudon and Brinklow, 1992), the enhanced growth would not persist and that, accordingly, the advantage of using 16L:8D must come from shifting the timing of seasonal growth rather than any additional growth *per se*. The present experiment has confirmed that this is indeed the case and after around 19 weeks the growth of animals under 16L:8D began to slow and the live-weight advantage over animals on natural photoperiod disappeared rapidly. A likely reason for this cessation of rapid growth is seen in the testes measurements which showed that testes development was also advanced by 16L:8D treatment and that peak testes size occurred at almost the same time that growth slowed in the 16L group. Advanced reproductive development is also indicated by higher FSH levels reported in red deer under 16L:8D (Davies *et al.*, 1995). An advancement of puberty with an earlier onset of the first rut, associated with the advancement of growth, may limit any long term live-weight advantage. The demonstration that the growth advantage under 16L:8D is temporary indicates that there is little advantage in placing replacement stock under 16L:8D, and the effects of altered seasonality in these animals, such as earlier puberty, may in fact cause management problems. The main advantage of the technique must arise from the shift in the time of growth i.e. increased value of stock that are ready for slaughter earlier.

In a previous study we showed that placing red deer calves under 16L:8D in autumn stimulated growth (Webster *et al.*, 1997a). In that study, the increase in photoperiod was around 5 h light per day. In the present study a similar increase in hours of light per day to the 13L group failed to stimulate rapid growth, suggesting that it is the duration of the photoperiod that is responsible for rapid growth rather than the size of the increase in light per day. While this result cannot definitely exclude the size of the increase as having a rôle, because it is possible that the critical increase necessary to stimulate growth may be greater in mid winter (when treatments were applied in the present study) than it is in autumn (previous study), it does provide further evidence that 16L:8D is particularly successful at initiating a rapid growth response.

There was very little difference in growth between animals on 13L, 11L, 8L or OC until mid December when OC began to grow faster than the other groups, particularly compared with 13L and 11L in which growth rate seemed to slow. This can be

interpreted in several ways. First, the similar growth patterns from June to December of animals on natural, 13L, 11L or 8L suggests that this phase of the growth cycle is not stimulated by photoperiod and is probably under endogenous control. Secondly, the divergence of OC from the other groups may have been an effect of photoperiod duration as it occurred after the natural photoperiod had exceeded around 14·5L and/or an effect of exposure to an unchanging photoperiod for a particular length of time, as growth slowed around the same time in 16L, 13L and 11L.

When comparing the responses of the groups to the different photoperiodic treatments it appears that there were two components to the response. An effect on the timing of the seasonal cycles and an effect on the amplitude of the seasonal cycles. First, effects on the timing of the seasonal cycles were evident in the earlier increases in prolactin, IGF-1, live weight and testes size of the 16L group compared with the OC group (an earlier increase in food intake in 16L *v.* OC was confounded by the higher food intake due to the environment of the outside group). The increase in photoperiod of 8 h, from 8L to 16L advanced seasonal cycles in 16L in an attempt to re-synchronize seasonal state with prevailing photoperiod. In the other groups which experienced smaller increases in photoperiod the advancement of seasonal cycles was more variable. There were earlier increases in prolactin and IGF-1 in 13L and a tendency for an earlier peak testes diameter but no advancement of food intake or live weight as in 16L. This partial response of 13L in comparison with 16L, may indicate that a photoperiodic effect on the timing of some components of the growth axis was detected but the photoperiod duration was insufficient to cause a full growth response. Different thresholds for different components of the growth response may produce a cascade of events that underlies the increase in growth as photoperiod lengthens in the spring.

An effect of photoperiod on the amplitude of seasonal cycles was evident in the 16L and OC groups which were exposed to photoperiods in excess of 13L and which showed higher amplitude peaks in live weight, food intake and testes size than the other groups. This may be due to an effect of photoperiod duration on IGF-1 and prolactin which were lower in 13L, 11L and 8L despite the apparent advancement in the timing of some of these cycles in 13L. Also of interest is the lower amplitude of the cycles in 8L, which presumably occurred under endogenous control as this group did not experience any increase in photoperiod, further suggesting an effect of photoperiod length on the amplitude of the growth cycle. This effect of duration of photoperiod

on the amplitude of the growth cycle is also seen when comparisons of growth patterns are made between populations of deer at different latitudes (Suttie and Webster, 1995) and a positive relationship was found between hours of daylight 60 days prior to the summer solstice and summer live-weight gain.

In conclusion, this study has confirmed the importance of using 16L:8D to stimulate rapid growth during winter in young male red deer. It has added to previous work in this area by showing that more than 13 h of light per day is necessary for the response and that the live-weight advantage is maintained until a target slaughter weight is attained approximately 7 weeks earlier. However if the animals are not slaughtered at this time, the live-weight advantage is lost by late summer. Increases in IGF-1 and prolactin are associated with the growth response and reproductive development is advanced along with growth.

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