Photoperiod, Appetite and Growth in Farmed Red Deer.

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Abstract

Winter inappetance is a major constraint to the productivity of farmed red deer Since growth and appetite in red deer are photoperiodically-dependant. it may be possible to prevent winter inappetance by providing artificially lengthened photoperiods throughout the winter A series of experiments was undertaken, in a winter-housed system in southern England, to investigate the feasibility of such use of artificial photoperiods to maintain winter growth rates

The effects of providing long days throughout the winter was investigated by housing red deer stags in long days (16L 8D) or ambient photoperiods from shortly after weaning until turn-out to pasture. Animals in long days grew faster through the early part of the winter, but growth rates declined in stags on long days in the last few weeks before turn-out in April (spring). When the interaction between plane of nutrition and daylength was also investigated, it was found that growth rate was greater in animals on long days than in those in ambient photoperiods during the winter, but that this situation was reversed towards the end of the housed period and after turn-out This effect was less marked in silage-fed deer than in those that also had received concentrates.

In further experiments, the effects of providing long days for only part of the winter was investigated Stags and hinds were exposed to long days until mid-winter (December) or February, whilst hinds were also exposed to long days from December or February to the time of turn-out Short-term exposure to long days did not affect growth, but exposure until February or from December resulted in a significant increase in growth and a marked advancement of slaughter date. Finally, stags were exposed to alternating long and ambient days, changing either every 3 or 6 weeks The 6-week alternation and, to a lesser extent, the 3-week alternation, advanced slaughter date compared with stags in ambient days, but neither was more effective than continuous long days

Plasma prolactin concentrations were not correlated with any parameters of growth, appetite or liveweight IGF-1 concentrations were related to patterns of appetite and, less strongly, to growth rate However, whether this was a causal relationship could not be determined. Finally FSH concentrations and antler lengths of stags in long days were greater than in those in ambient days

It was concluded that exposure to long days during the winter increases winter growth rate by preventing the development of winter inappetance Of the photoperiodic regimes that were tried, long days until February resulted in the greatest potential reduction in slaughter date. However, for the benefits of this regimen to be maximised, although 80 kg is an appropriate slaughter weight for hinds, a reduction of the slaughter weight of stags from 100 to 90 kg would be allow the greatest benefit of the programme to be reaped.

Context

The experiments reported in this paper were undertaken between 1991 and 1995, at Rosemaund Experimental Husbandry Farm, Hereford, UK, in collaboration with Mervyn Davis and David Deakin. The work was supported by funding from the EU. The role of the Author in these studies was in the endocrine assessments and as a participant in the design of the photoperiodic regimens that were used The studies were undertaken by the staff of the Rosemaund EHF, under approval of the Animals (Scientific Procedures) legislation of the UK Davis et al (1995) first reported these data, in part

Introduction

Many aspects of the biology of animals are seasonally regulated. Probably the best-known example is reproductive seasonality, since, at least in domestic animals, this can cause a significant constraint to their economic performance. Sheep, goats and red deer are fairly strictly seasonal, although far less so than some of the extreme seasonal breeders that are found amongst wild birds (Nicholls *et al*, 1988) Several other aspects of biology are controlled by daylength Not surprisingly, hibernation is controlled in this way, but so is migratory behaviour in migratory birds The hyperphagia that hibernating and migratory species exhibit before they embark of these activities is also photoperiod-dependent· all of these behaviours can be manipulated by manipulations of daylength

The constraints that seasonality imposes upon deer farming are not solely confined to those upon reproductive activity Antler growth, linked as it is to the reproductive endocrine axis, is obviously limited by season, but so too is appetite, food intake and growth. Indeed, the constraint imposed upon deer farming by such seasonal limits upon growth is probably of no less importance than reproductive seasonality, since, during the period of winter inappetance, red deer calves stop growing or even lose weight Clearly, this is a major problem for semi-intensive deer production, especially in the economic climate of European deer farming, with its high housing costs and competition from culled wild deer and imported venison

The phenomenon of winter inappetance in deer has been recognised for some time Winter inappetance was first reported in white-tailed deer by French *et al* (1956) and a number of reports have been made of the same phenomenon in red deer (e g Blaxter *et al*, 1974, Pollock, 1975, Moore and Brown, 1978). Kay (1979) demonstrated that the patterns of food intake and growth are photoperiod-dependent by subjecting stags to photoperiodic regimens in which the annual cycle of daylengths was compressed into 6 months Appetite was highly correlated with daylength Simpson *et al* (1984) also reported similar, but slightly less dramatic results

In consequence, a number of studies have attempted to abrogate the winter inappetance by maintaining slaughter-generation deer under fixed photoperiods of long days Typically, these have provided daylengths equivalent to the summer solstice (16 hours of light and 8 hours of dark in each 24-hour period. 16L.8D) For example, Webster *et al.* (1999) kept stags on 16L:8D from the time of the summer solstice (January), throughout the following autumn and winter. Their results were very interesting, in that growth rate was slightly higher in control than treated animals in the initial period of daylength manipulation, but thereafter, the long-day animals overtook the control animals More interesting still was that the long-day animals ceased their accelerated growth by April and, by June there was again no difference between groups

Preliminary investigations

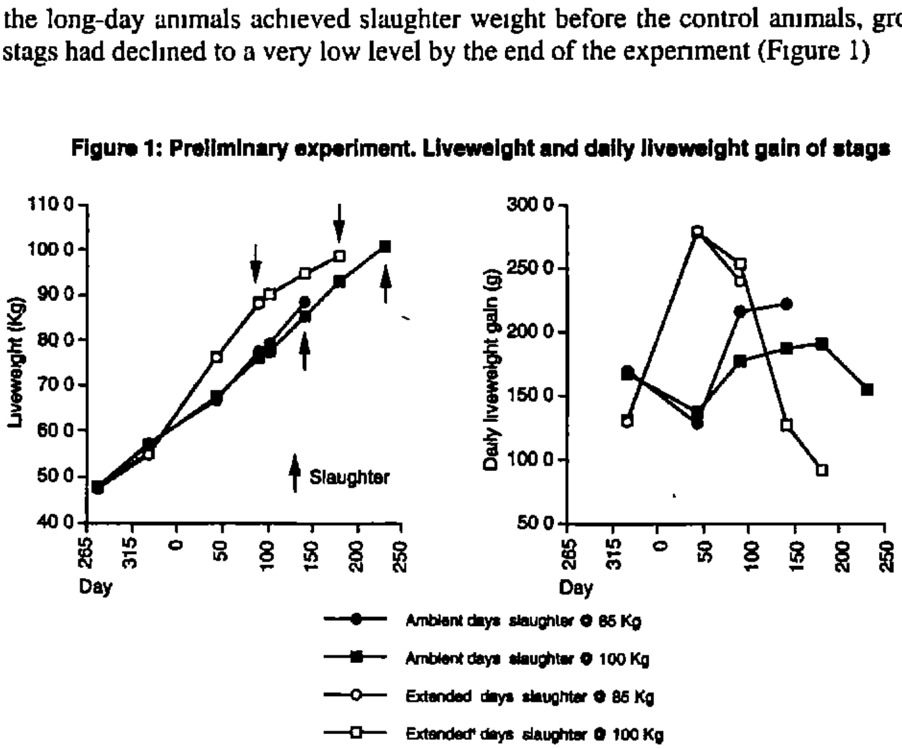
A preliminary experiment by the author and co-workers had found similar responses to long days some time previously (Davies *et al*, 1995) Stags calves were housed in long days (16L·8D) or ambient photoperiods (52°N) from the autumn equinox (mid September) until the following spring

Material & Methods (Preliminary Experiment)

- Spring-born red deer stag calves (n=20/group)
- Housed from weaning (late August)
- Ambient days or 16L:8D
- Fed silage + 1 kg concentrate (80% barley, 20% soya)
- 10 of each group slaughtered at 85 kg l wt
- the remainder slaughtered at 100 kg l wt

During the first 6 weeks after housing, stags in long days had a slower growth rate than those in ambient photoperiods Thereafter, the long-day animals overtook the control animals. However, by February, growth rates in control stags had again overtaken those of the long-day animals, and, although the long-day animals achieved slaughter weight before the control animals, growth rates in long-day stags had declined to a very low level by the end of the experiment (Figure 1)

Figure 1: Preliminary experiment. Liveweight and daily liveweight gain of stags



A second, similar experiment was undertaken in the following year, which investigated the patterns of growth of stags in more detail, compared this growth in hinds, and investigated whether the effects of photoperiod were moderated by plane of nutrition The mechanism by which photoperiod regulated growth was also of interest, so a number of metabolically-active hormones which are known to be affected by photoperiod were measured, so that they could be correlated with the patterns of growth.

Material & Methods (Experiment 1)

- Spring-born red deer stag and hind calves (n=10/group)
- Housed from weaning (late September)
- 2x2 factorial design:
- Ambient days or 16L:8D
- Fed silage alone or silage + 1 kg concentrate
- DMI continuously monitored Weighed every 2 weeks
- Blood sampled every 2 weeks to measure [prolactin, IGF-1, FSH and (in stags) testosterone]
- Stags slaughtered at 100 kg l wt, hinds at 80 kg l wt

The liveweights and daily liveweight gains of stags are shown in Figure 2, and those of hinds are in Figure 3. Stags and hinds exhibited very similar patterns of growth such that, after an initially higher rate of growth in animals in ambient days, there was a much higher growth rate in stags and hinds in daylengths of 16L:8D As expected, growth rates were higher in animals that received concentrates than in those that had silage alone

All groups of deer that were on 16L 8D exhibited reduced growth rates over the last weeks of the housed period Both stags and hinds that had been on the higher plane of nutrition in daylengths of 16L·8D exhibited a very significant check to growth after turnout Animals which had been on long days but had not received concentrates exhibited a less serious growth check As a result, the dramatic difference between the liveweights of deer in ambient days and long days which was present at the end of the housed period had largely disappeared by the time the animals were slaughtered Deer that had been housed in ambient days also exhibited a period of very rapid growth after turn-out, which was actually greater than the growth rates that were achieved during the winter by animals in long days Of the stags that received concentrates, mean slaughter date was 16 days earlier for the animals on long days through the winter than those on ambient days The situation was reversed for stags that received only silage

Figure 2: Experiment 1. Liveweight and daily liveweight gain of stags

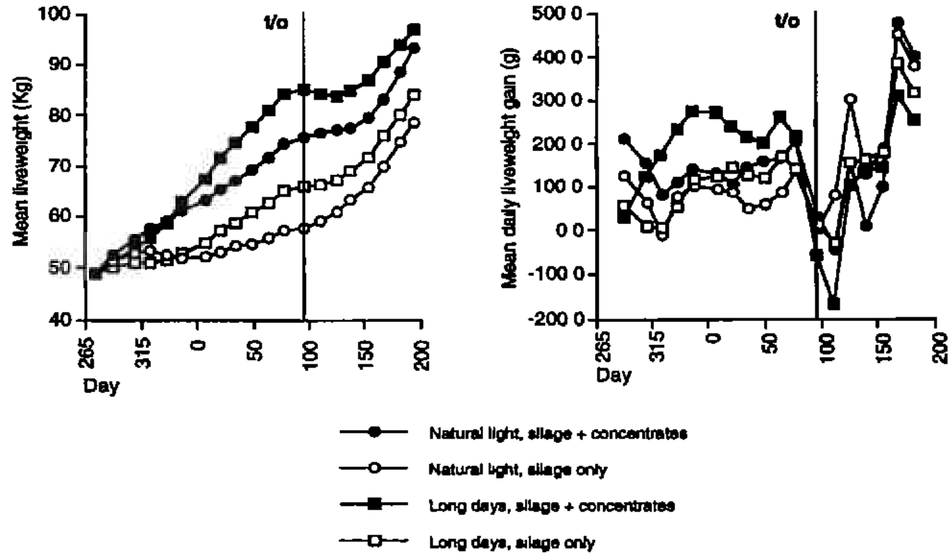
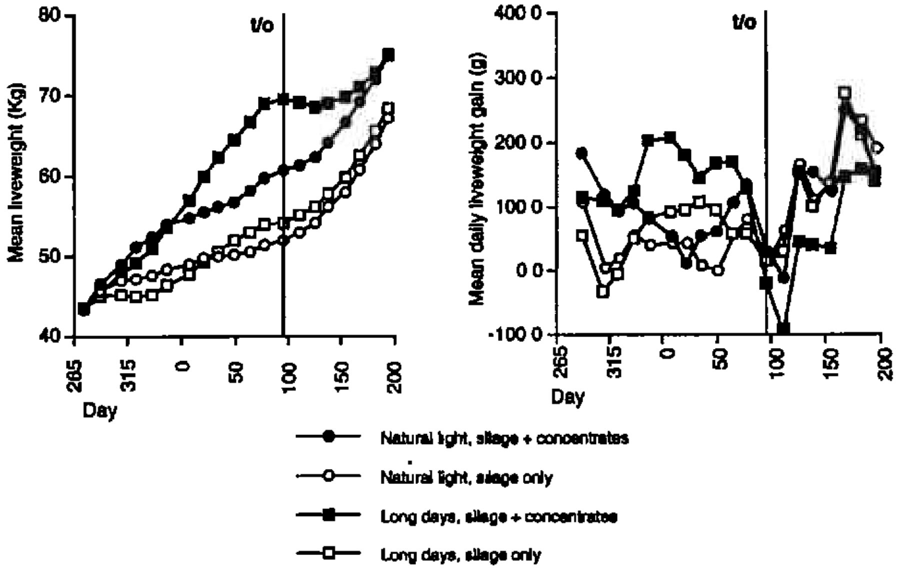


Figure 3: Experiment 1. Liveweight and daily liveweight gain of hinds



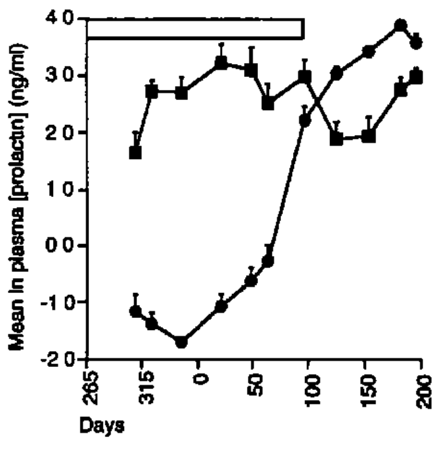
Concentrations of prolactin were highly related to the photoperiod to which the deer were exposed (Figure 4). However, correlations between prolactin concentrations and growth rate were weak in stags and non-existent in hinds Concentrations of IGF-1 were, however, correlated with growth rate (mean daily liveweight gain) and strongly correlated with dry matter intake. FSH concentrations were higher throughout the winter in stags housed in long days than in ambient days, but there was a marked increase in FSH concentration in ambient-day stags after turn-out. Testosterone concentrations of stags were unrelated to treatment regimen

Thus, although there was a great increase in growth rate during the period of exposure to long days, the gains that were achieved by photoperiodic manipulation were largely lost during the final period of housing and after turn-out This effect was worse in animals on a higher plane of nutrition than in those on a lower plane.

Stopping growing: daylength at turn-out or photorefractoriness?

The reasons for the results to the two previous experiments have to be understood with reference to the mechanisms that regulate seasonality Most seasonal phenomena persist in the absence of photoperiodic drivers One of the best-known examples of such a phenomenon is the annual cycle of testis growth and regression in the domestic ram Howels *et al.* (1982) kept rams in constant photoperiods for three years Initially, they responded to the daylength into which they had been placed (i e. with testis growth in short days, or testis regression in long days). However, a circannual (i.e. approximately of annual duration) cycle of growth and regression established itself in both groups of rams, such that the animals which had initially undergone testis growth, then went through a phase of regression which was, in turn, followed by a further phase of growth. The converse occurred in animals on perpetual long days

Figure 4: Experiment 1. Plasma prolactin profiles of stags in ambient photoperiods and on 16L:8D throughout the winter



The horizontal bar indicates the period of exposure of the 'long day' group to a16L 8D photoperiod

The explanation of such results seems to be that seasonality is not driven by external cues, such as photoperiod, but is internally generated (Nicholls *et al* , 1988) Thus, the breeding season of the sheep or of the red deer is of fixed duration and, whilst its onset can be controlled by photoperiodic manipulation, its duration cannot be readily manipulated Hence, if a ram is removed from ambient long days into constant short days, they will become sexually active However, after a few months, they will become refractory to short days and their breeding season will end (Robinson and Karsch, 1985). Testicular regression therefore follows whilst the ram is refractory to short days The phenomenon of photorefractoriness is seen even more clearly in seasonally-breeding birds For example, the starling (*Sturnus vulgaris*) is a long day breeder, whose breeding season starts soon after daylength starts to increase after the winter solstice However, after a few weeks of sexual activity, their breeding season ceases, a long time before the longest day has been reached. In other words, starlings become refractory to the stimulatory effects of long days after just a few weeks. Even though daylength continues to increase, it is unable to re-start or prolong the breeding season, as the birds have become unresponsive to its effects (Goldsmith *et al*, 1989)

Hence, seasonal phenomena such as reproductive activity, growth etc, should be considered as manifestations of endogenously generated rhythms, which are synchronised with climatic season by the effects of photoperiod.

It was postulated that the responses to the photoperiodic regimens used in the first two of the present experiments could be explained in terms of photorefractoriness Thus, although deer would show an increased appetite, in response to exposure to long days, the eventual diminution (or cessation) of this response would be as predicted if the animals were to have become refractory to long days Moreover, it would also be expected that growth rates in the deer housed in ambient days would overtake those of the long-day animals, since growth rates in the former would be positively photostimulated whereas, in the latter, they would be declining to a level that was equivalent to that of animals during normal winter photoperiods.

An additional problem of using a 16L.8D lighting regime to promote appetite during the winter occurs at the time of turn-out. Turn-out is often associated with a check to growth rates, largely due to a change of diet from conserved feed (± concentrates) to lush, spring grass As importantly, daylength at the time of turn-out is closer to 12L 12D than 16L 8D, so, even though ambient photoperiods would be increasing, the deer would actually experience a *reduction* in daylength. Thus, deer exposed to long days during the winter could not only become photorefractory to long days by the end of the winter, but could also perceive that they have been placed in short days at the time of turn-out.

Can complicated photoperiodic regimes eliminate refractoriness and the 'turn-out' effect?

The duration of photoperiod-driven events is remarkably difficult to alter. Most manipulations rely upon altering the time of onset of the event rather than its duration Thus, melatonin implants bring sheep into their breeding season sooner the duration is unaffected, so they also go out of season sooner (Robinson *et al*, 1992) This, a further consequence of refractoriness (or, put another way, of seasonality being an endogenously created rhythm of fixed duration), can only be prevented by the use of complicated photoperiodic regimens Thus, refractoriness can be overcome by (in the case of breeding season of sheep) the use of yet shorter daylengths when the animals become refractory to short days (Nicholls *et al*, 1989) Likewise, photoperiodic regimens in which daylengths change at relatively short intervals may prevent the development of refractoriness (Pelletier and Almeida, 1987). As discussed later, work with rams has shown those rapid alterations of daylengths between long and short days can indefinitely prolong the breeding season

Experiments were therefore undertaken to see if the problems encountered at the end of the winter and at turn-out in the previous experiment could be prevented by the use of more complicated photoperiodic regimens, which would attempt to prevent refractoriness from developing It was also postulated that, if animals were exposed to altering photoperiods during the winter, they might be less inclined to perceive the change from long days to ambient days at the time of turn-out as a change into short days

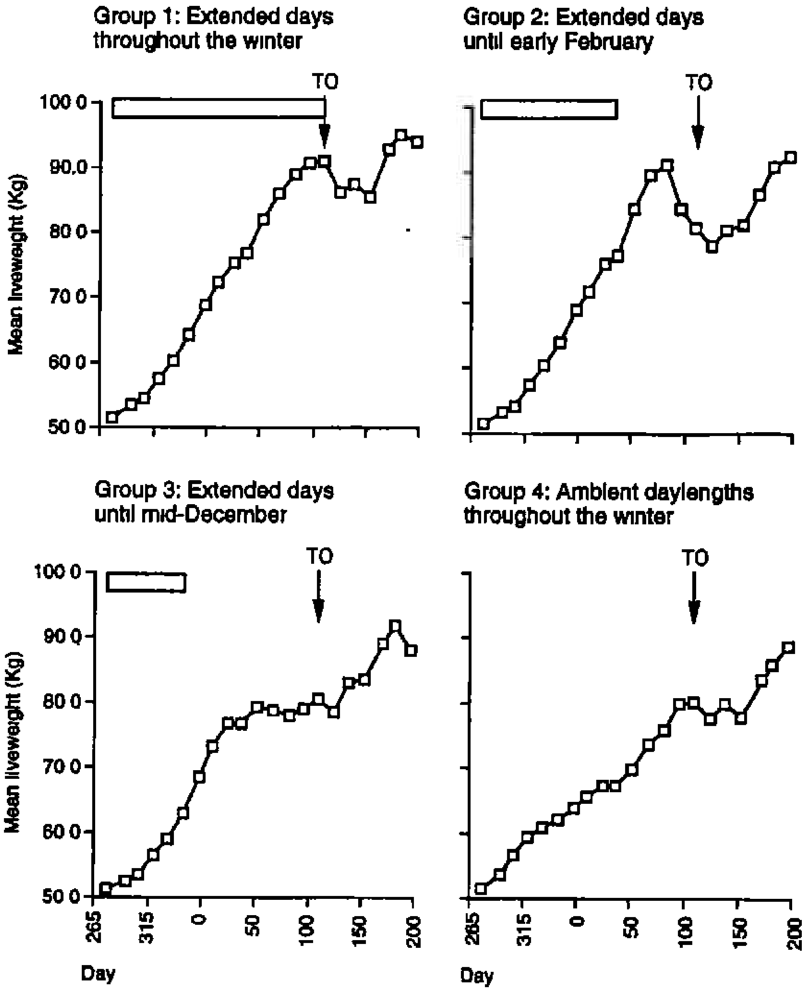
Material & Methods (Experiment 2)

- Spring-born red deer stag calves (n=10/group)
- Weaned in August, housed from mid-September
- 4 photoperiod regimes

- 16L·8D until turn-out
- 16L 8D until early-February, then ambient days
- 16L 8D until mid-December, then ambient days
- Ambient days throughout the winter
- Fed silage alone or silage + 1 kg concentrate
- DMI continuously monitored. Weighed every 2 weeks
- Blood sampled every 2 weeks to measure [prolactin, IGF-1, FSH and testosterone]
- Slaughtered at 100 kg l wt

Growth rates were much faster in stags on long days that in those on short days throughout the winter (see Figure 5)

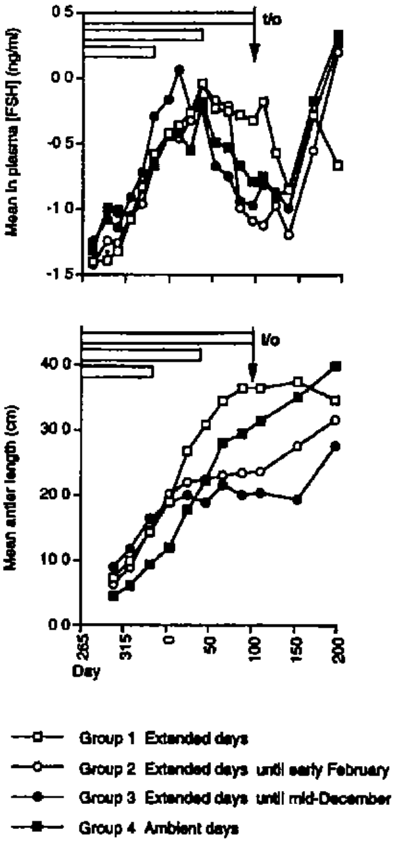
Figure 5: Experiment 2. Liveweights of stags



The groups of animals that were on long days for part of the winter had high growth rates during their exposure to long days Stags on long days throughout the winter lost weight at turn-out, but their weight remained ahead of the animals on ambient days until mid-June Deer on extended days until February underwent a considerable loss of weight, which started shortly after the transition from long to ambient days (i.e going from 16L 8D to about 10L.14D), but which lasted so long that liveweights had not returned to maximal values until 150 days after the start of weight loss. The most interesting group was the one on long days until mid-December These animals, despite a huge change in daylengths, did not lose weight after the transition, nor did they have a weight-gain check at turn-out. Nevertheless, stags exposed to long days for part of the winter had earlier mean slaughter dates than animals that experienced long days throughout the winter Stags on ambient days had the latest slaughter date Had a 90 kg slaughter weight been chosen for the stags, the group on long days until February would have had by far the earliest slaughter date (late March) However, the losses of weight between this time and turn-out, and in the post turn-out period were such that they did not reach the 100 kg target until August

Treatment	Peak weight pre turn-out (kg)	Mean weight at turn-out (kg)	Mean slaughter date
Continuous 16L 8D	90 9 (turn-out)	90 9	16 August
16L 8D until December	80 5 (turn-out)	80 5	3 August
16L'8D until February	91 2 (22 March)	81 5	4 August
Ambient days	80 3 (turn-out)	80 3	13 September

Figure 6: Experiment 2. FSH concentrations and length of antler-buds in stags



As in the previous experiment, prolactin concentrations reflected daylength, and were unrelated to any parameters of growth or appetite. However, unlike the previous experiment, there was no correlation between IGF-1 concentrations and any parameters of growth, although concentrations did decline markedly in some groups during periods of weight loss (Figure 9) FSH concentrations (Figure 6) were again higher in stags during periods of long days, but there was no simple relationship between testosterone concentrations and treatment regimen Interestingly, antler-bud growth was most rapid in the stags on long days throughout the winter, although growth stopped at same time as did liveweight gain

Antler-bud growth in stags which were exposed to extended days for part of the winter ceased with the transition back into ambient days Antler-bud growth had been slowest in the stags on ambient days throughout the winter, but there was no check to growth at turn-out, so they ended up with the largest, fastest-growing antler-buds

In the following year, the effects of exposing deer to extended photoperiods at different stages of the winter were further explored The rationale was two-fold Firstly, the results from the stags on long days until February were so remarkable, it seemed sensible to make sure that this result was repeatable Secondly, the effects of providing long days in the later part of the winter had not been studied in the previous experiments Since there was a consistent period, at the start of the housing period, when animals on long days had lower growth rates than those on ambient days, it was postulated that, if long days were applied later in the season, it might be possible to avoid this period of suppressed growth

Material & Methods (Experiment 3)

- Spring-born red deer hind calves (n=9/group)
- Weaned in August, housed from mid-September
- 5 photoperiod regimes
- 16L 8D until early February, then ambient days
- 16L 8D until mid-December, then ambient days
- Ambient days until early February, then 16L 8D
- Ambient days until mid-December, then 16L 8D
- Ambient days throughout the winter
- Fed silage alone or silage + 1 kg concentrate
- DMI continuously monitored Weighed every 2 weeks.
- Blood sampled every 2 weeks to measure [prolactin, IGF-1 and FSH].
- Slaughter planned at 80 kg l wt

The deer used in this experiment were to have been slaughtered at 80 kg liveweight. In the event, other factors required that they were retained. Hence, additional criteria were used to judge the effectiveness of the treatments, namely, weights at the time of turn-out and the time take to reach a liveweight of 80 kg

Liveweights of hinds in Experiment 3 are shown in Figure 7 All hinds exposed to long days from the time of housing had lower growth rates than animals kept in ambient days for the first two months of the trial. Subsequent growth rates were higher in hinds kept in long days. The hinds which were exposed to long days until December ceased to grow for about 6 weeks after the transition back to ambient days Thereafter, their liveweights were identical to those of animals kept in ambient days throughout the winter. Hinds kept in long days until February grew very rapidly, reaching a group mean weight of 80 kg on 14th March - 4 weeks before turn-out. If each deer had been slaughtered when it reached 80 kg, the mean slaughter date would have been 22nd May. Although these animals did exhibit a significant loss of weight after turnout, this would have been of no practical consequence, since they would have long since reached slaughter weight Growth rates of hinds exposed to long days after February were indistinguishable from those of animals kept in ambient days, but exposure to long days after December significantly increased growth rates and shortened the time to presumptive slaughter date

Treatment	Mean weight at turn-out (kg)	Proportion of animals >78 kg at turn-out	Date of group mean weight > 80 kg	Mean date of individual live-weight >80 kg
Ambient days	69 5	1/9	24 July	31 July
Long days from February	70 1	1/9	23 August	13 August
Long days from December	74 8	2/9	23 August	16 July
Long days to December	70 4	0/9	23 August	18 August
Long days to February	80 1	6/9	24 March	22 May

As in previous experiments, prolactin concentrations were unrelated to any parameters of growth or appetite IGF-1 concentrations were only weakly correlated with dry matter intake and were unrelated to other parameters of growth. There were no clear patterns of FSH secretion

Material & Methods (Experiment 4)

- Spring-born red deer stag calves (n=10/group)
- Weaned in August, housed from mid-September
- 4 photoperiod regimes
- 16L 8D throughout the winter
- 16L 8D and ambient photoperiods, alternating every 6 weeks throughout the winter
- 16L 8D and ambient photoperiods, alternating every 3 weeks throughout the winter
- Ambient days throughout the winter
- Fed silage alone or silage + 1 kg concentrate
- DMI continuously monitored. Weighed every 10 days.
- Blood sampled every 10 days to measure [prolactin, IGF-1, FSH and testosterone].
- Slaughtered at 100 kg l.wt

Finally, the work of Pelletier and Almeida (1987) was used as a rationale for exposing deer to a frequently-alternating photoperiodic regimen as a means of preventing the development of photorefractoriness In their studies, progressively changing photoperiods between long and short days every two months virtually abrogated the photoperiod-driven changes in testicular weight, with testes being maintained at a size close to that of the normal annual maximal value.

Since facilities did not exist in our deer accommodation for providing continuously varying photoperiods, it was decided to provide a photoperiodic regimen in which daylengths changed abruptly between ambient days and 16L 8D at either 6-weekly or 3-weekly intervals

Figure 7 : Experiment 3. Liveweights of hinds

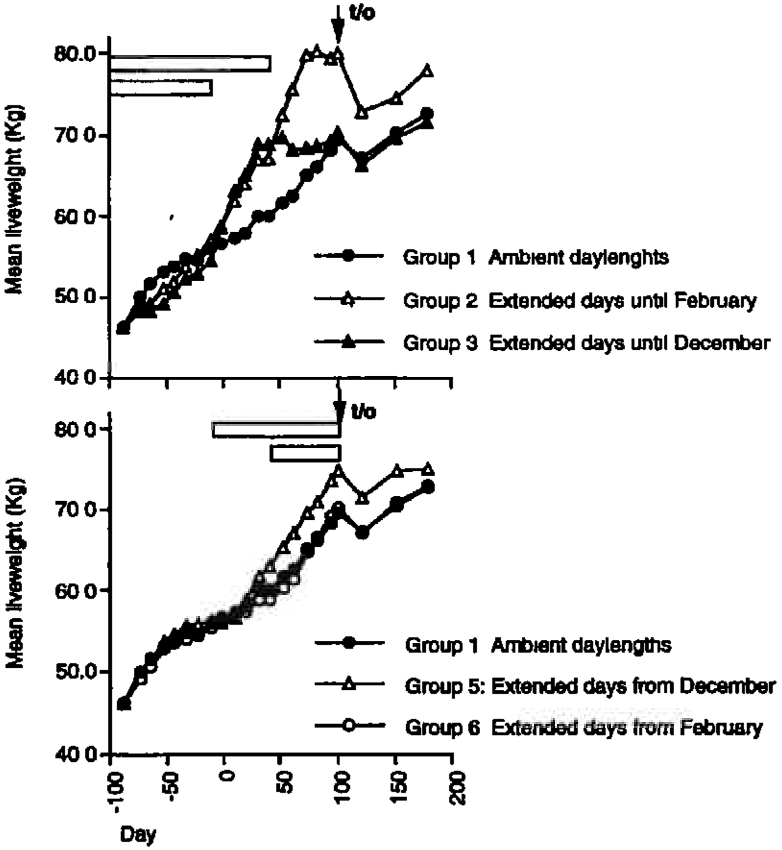
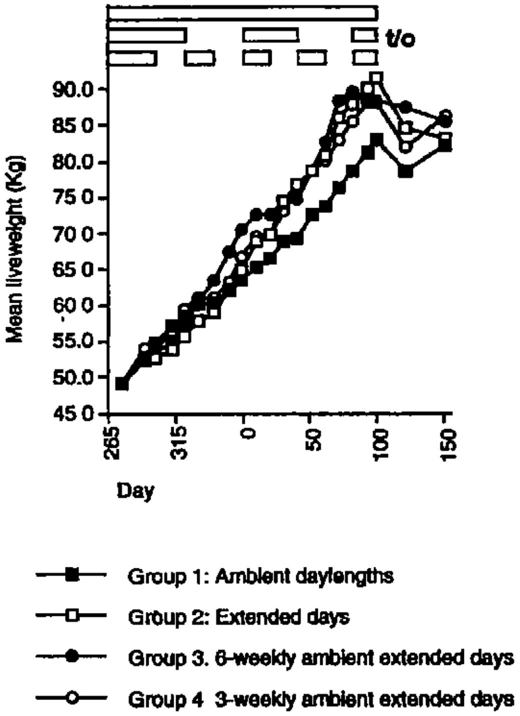


Figure 8 : Experiment 4. Liveweights of stags



▭ Periods of housing in 16L 8D photoperiods

Figure 9: Experiment 2. Temporal relationships between IGF-1 concentrations and daily liveweight gain

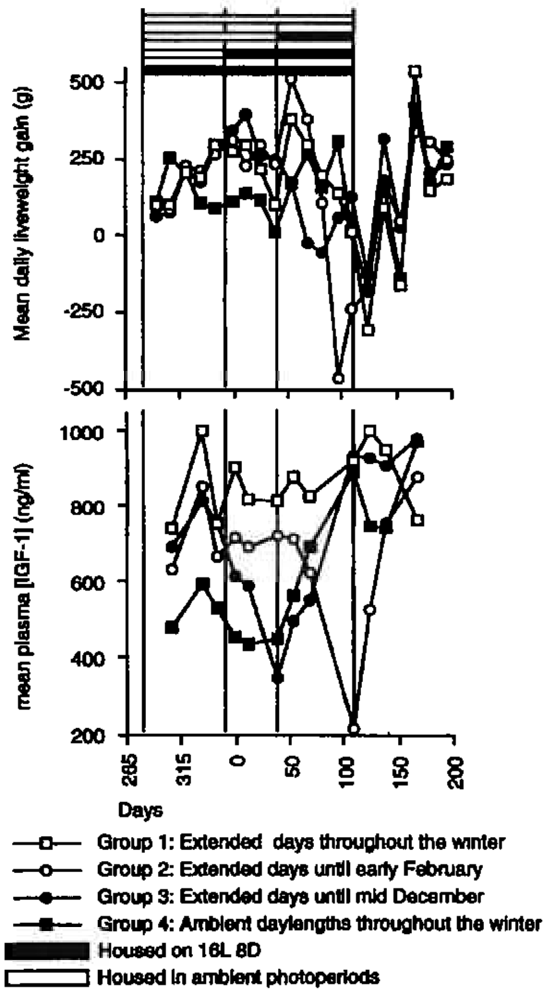
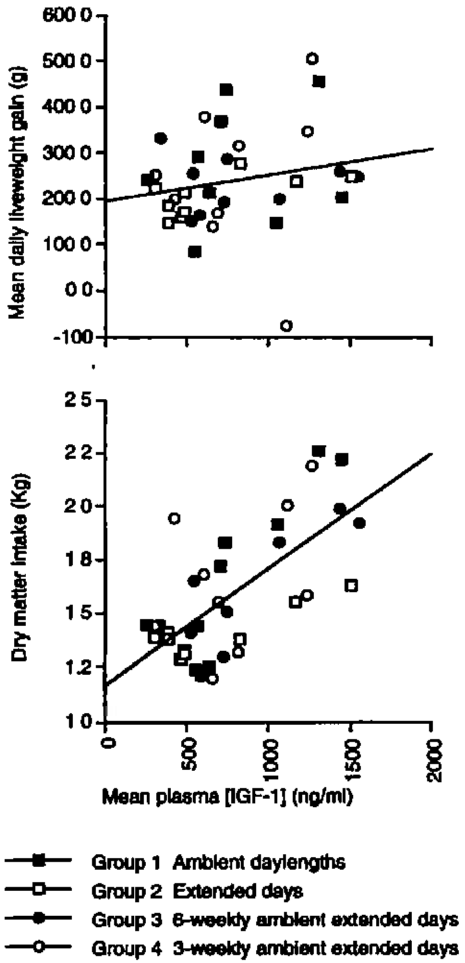


Figure 10: Experiment 4. Relationship between IGF-1 concentrations and (a) daily liveweight gain and (b) dry matter intake of stags



As in the previous experiment, stags on long days throughout the winter grew faster than those on ambient photoperiods (Figure 8). Unlike the previous trials, there was no cessation of growth in these animals during the last few weeks of the winter, so their liveweight at turn-out was significantly greater than in deer on ambient photoperiods However, all stags (including those that had been on continuous long days) did experience some loss of weight in the period of time after turn-out However, by 3 weeks after turn-out, liveweights of stags that had been in ambient photoperiods and on 6-weekly alternations were above those at turn out Only the animals on 3-weekly alternation were still significantly lighter than before turn-out

Treatment	Mean weight at turn-out (kg)	Mean weight 3 weeks after turn-out (kg)	Mean slaughter date
Continuous 16L 8D	91 5	90 8	29 May
6-week alternation 16L 8D /ambient	88 3	89 9	4 June
3-week alternation 16L 8D /ambient	88 2	85 7	2 July
Ambient days	83 0	81 0	28 July

Again, there was no relationship between prolactin concentrations and parameters of growth or appetite. There was a weak correlation between IGF-1 concentrations and growth rate, and a stronger correlation with dry matter intake (Figure 10) FSH concentrations were higher in stags on 6-weekly alternation than in other animals during the last month of the housed period Concentrations were not measured after turn-out There were no differences in the rate of antler bud growth between treatments, nor was there any clearly-discernible pattern of testosterone concentrations

Conclusions

The winter period of low growth rates is driven by declining photoperiod and can be reversed, at least for a while, by exposure to long days. The slower growth is itself the consequence of reduced voluntary feed intake (Suttie *et al*, 1984, Loudon *et al*, 1989), which is caused by the eating of smaller meals at longer intervals between meals (Rhind *et al*, 1998) The effect is probably independent of the availability of feed (Fennessy, 1982), but conflicting evidence exists (Heydon *et al*, 1993)

The present experiments demonstrate that growth rates can be maintained at much higher levels in stags and hinds that are maintained on, or have intermittent exposure to, long days (16L:8D) throughout the winter However, other than in Experiment 4, all of the deer that had been exposed to long days throughout the winter ceased to maintain high growth rates until the time of turn-out. A number of other studies have demonstrated higher growth rates in deer that are exposed to long days during the winter (Suttie *et al*., 1992a, Webster *et al*, 1998, 1999) and, as in the present work, most have also found that the beneficial effect of long days wears off after about 4 to 6 months This is compatible with both the notion that the deer become refractory to long days after this period of exposure and the observation of Simpson *et al* (1983) that there is an endogenous rhythm of appetance/inappetance which cannot wholly be abrogated by the photoperiodic regimens to which the deer are exposed

The stimulatory effect of long days upon appetite occurs whether the deer are photostimulated from the time of the winter solstice (Webster *et al*, 1998), the autumn equinox (as in the present results), or even when calves are exposed to extended daylengths from birth (Simpson *et al*, 1984). Interestingly, in the work of Suttie *et al.* (1984, 1992a) and of Webster *et al* (1998), stimulation of growth rate did not occur when stags were exposed to daylengths of less than 16L 8D during the winter, for there was no increase in growth rate in animals exposed to 13 25L·10 75D Likewise, modest changes in daylength around the time of the winter solstice also failed to significantly affect growth (Webster *et al*, 1997) Whilst it is unclear why a small increase in daylength was ineffective in stimulating growth and appetite, it may be a reflection of the power of the endogenous rhythm and the degree of photostimulation that is needed to reverse the effect

Most of the aforegoing studies maintained animals under photoperiodic stimulation for long periods, whereas, in the present work, deer were turned-out to pasture after about 6 months, just after the spring equinox. Thus, they were transferred from 16L 8D to a daylength of little more than 12L.12D. This would be perceived as a transition into short days, since the perception of daylength is generally regarded as being relative to the previous photoperiods, rather then as an absolute duration of light/darkness Hence, deer which had been exposed to long days throughout the winter not only were refractory to long days before the time of turn-out, but were also exposed to a photoperiod after turn-out which they would perceive as inhibitory. In other words, the result of exposure to long days throughout the winter was to delay the onset of 'winter' inappetance by 5 to 6 months, rather than to abrogate the phenomenon completely

The responses to the regimens that exposed deer to long days for only part of the winter were therefore of considerable interest Exposure to long days between the time of housing and February (Experiment 2· stags, Experiment 3. hinds) was as effective at maintaining growth rates through the winter as was exposure throughout the winter In both experiments, high liveweights were achieved by the end of the winter period For the hinds in Experiment 4, sufficiently high group mean weight was achieved to have allowed slaughter in late March, the same date as stags achieved a group mean liveweight of 90 kg Given that it then took the stags until August to reach the 100 kg target, due to subsequent weight losses, slaughtering at 90 kg seems far more economically viable for such animals than waiting until they have reached the higher weight The responses to the rapidly alternating photoperiods of Experiment 4 were also of interest A 6-week alternation significantly increased growth rates above those of animals in ambient days, but it was not entirely clear how effective this method was, since the animals on continuous long days did not exhibit the expected drop in growth rates before turn-out The 3-week alternation was less effective than the other two regimens

The lack of relationship between prolactin concentrations and growth /appetite was not expected, given the strong relationship between each of these factors and daylength Moreover, in red deer (Suttie and Key, 1985, Curlewis *et al*, 1988, Webster *et al*, 1999) and in various other species, relationships between prolactin concentrations and appetite have been demonstrated. However, Milne *et al* (1990), who administered dopamine agonists and antagonists to red deer, were unable to relate changes in prolactin concentrations with effects upon appetite, so, perhaps, the situation is not entirely straightforward. On the other hand, IGF-1 concentrations were closely related to appetite and less strongly so to daily liveweight gain Since growth hormone and IGF-1 are as much dependent upon plane of nutrition as they are determinant of it, the present results do not shed a lot of light on whether the GH/IGF-1 system is likely to be of importance in the generation of the phenomenon of winter inappetance Even though the work of Suttie *et al* (1992b) appears to provide definitive evidence for a direct effect of photoperiod upon these hormones and Webster *et al* (1996) have associated season and growth patterns with GH/IGF-1 patterns, Ryg and Langvatan (1982) suggested that GH secretion was more related to antler growth and casting than to photoperiod *per se*. However, even this conclusion was questioned by the results of Barrell *et al* (1985), so the role of the system in the generation of winter inappetance is most unclear Interestingly, the present results seem to be at variance with the work of Adam *et al* (1996), who considered that IGF-1 was more closely related with photoperiod in female than male red deer

Finally, the effects of photoperiod upon antler growth were largely as expected No other reports of FSH concentrations in red deer were found

Summary

Winter growth rates of stags and hinds are increased in photoperiods of 16L 8D

After >5 months exposure to long days, growth becomes photorefractory and inappetance ensures

Turn-out from 16L.8D to ambient photoperiods during April is associated with inappetance, resulting in weight loss This is due, at least in part, to the transition into shorter days

Exposure to long days between September and February allowed hinds (and, potentially stags) to reach slaughter-weight in March, five months before animals housed in ambient days

Six-weekly alteration between long days and ambient daylengths also reduced the time to slaughter

Winter inappetance cannot be explained in terms of prolactin concentrations. It is unclear whether changes in IGF-1 concentrations cause, or are caused by, changes in appetite.

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