

Photoperiod effects on the development of beef heifers

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Small, J. A., Glover, N. D., Kennedy, A. D., McCaughey, W. P. and Ward, D. R. 2003. **Photoperiod effects on the development of beef heifers.** *Can. J. Anim. Sci.* **83**: 721–730. Crossbred beef heifers ($n = 144$) were assigned at weaning (187 ± 14 d of age) by body weight (225 ± 23 kg) and sire breed (British/Continental) to one of two photoperiod treatments from 21 December 1998 (0 wk) until 10 May 1999 (20 wk): natural photoperiod (NP) that gradually increased from 8.1 h (0 wk) to 15.2 h (20 wk) and, extended photoperiod (EP) that consisted of natural + supplemental light (400 lx, 1 m above ground) to extend photoperiod to 16 h. Rations were formulated for two-steps of body weight gain (0.6 and 1.2 kg d⁻¹) to achieve 60% of mature weight at 18 wk. Visual observations of estrus behavior were made twice daily and confirmed by serum progesterone. Body weight, backfat and serum prolactin data were determined for each 4-wk period. Ambient temperatures averaged $-12.2 \pm 6^\circ\text{C}$ in winter (0 to 12 wk) and $4.2 \pm 5^\circ\text{C}$ in spring (12 to 20 wk). Gain in body weight was greater ($P < 0.05$) and backfat lower ($P < 0.05$) for EP than NP treatments from -2 to 6 wk and only 1% of heifers had attained puberty during this period. However, as yearlings at similar ($P > 0.05$) body weight and backfat, more ($P < 0.05$) EP than NP heifers had attained puberty (84.7% vs. 69.4%). Prolactin was greater ($P < 0.05$) for EP than NP treatments from 2 to 6 wk (10.3 vs. 5.5 ± 1.2 ng mL⁻¹). Management of photoperiod influences attainment of puberty and prolactin secretion in beef heifers housed in an outdoor environment.

Key words: Photoperiod, puberty, estrus, beef heifers, prolactin

Small, J. A., Glover, N. D., Kennedy, A. D., McCaughey, W. P. et Ward, D. R. 2003. **Incidence de la photopériode sur la croissance des génisses de boucherie.** *Can. J. Anim. Sci.* **83**: 721–730. Au sevrage (187 ± 14 jours), les chercheurs ont réparti des génisses de boucherie hybrides ($n = 144$) en deux groupes selon le poids (225 ± 23 kg) et la race du géniteur (britannique/continentale). Chaque groupe a ensuite été affecté à deux régimes d'éclairage du 21 décembre 1998 (semaine 0) au 10 mai 1999 (20^e semaine) : une photopériode naturelle (PN), où l'éclairage a progressivement augmenté de 8,1 h (semaine 0) à 15,2 h (20^e semaine), et une photopériode prolongée (PP) avec éclairage d'appoint (400 lux à 1 m du sol) pour porter la durée de l'éclairage à 16 h. Les rations ont été préparées de manière à permettre un gain de poids en deux temps (0,6 puis 1,2 kg par jour) et pour que les animaux atteignent 60 % de leur poids adulte à 18 semaines. Deux fois par jour, on a déterminé visuellement si les génisses étaient en chaleur puis confirmé le résultat par dosage de la progestérone du sang. Les chercheurs ont mesuré le poids corporel, l'épaisseur du gras dorsal et la concentration de prolactine sérique à intervalles de quatre semaines. La température ambiante s'établissait en moyenne à $-12,2 \pm 6^\circ\text{C}$ en hiver (semaines 0 à 12) et à $4,2 \pm 5^\circ\text{C}$ au printemps (12^e à 20^e semaines). De la semaine -2 à la 6^e semaine, le régime PP a entraîné un meilleur gain de poids ($P < 0,05$) et une plus faible épaisseur du gras dorsal ($P < 0,05$) que le régime PN et 1 % seulement des génisses avaient atteint la puberté à ce moment. Néanmoins, quand les animaux d'un an ont un poids et une couche de gras dorsal similaires ($P > 0,05$), on compte plus de génisses pubères ($P < 0,05$) avec le régime PP que le régime PN (84,7 % c. 69,4 %). La concentration de prolactine était plus élevée ($P < 0,05$) avec le régime PP que le régime PN de la 2^e à la 6^e semaine (10,3 c. $5,5 \pm 1,2$ ng par mL). On en conclut que la photopériode exerce une influence sur la puberté et la sécrétion de prolactine chez les génisses à viande gardées à l'extérieur.

Mots clés: Photopériode, puberté, œstrus, génisses de boucherie, prolactine

Business risk in the cow/calf sector of the beef industry is reduced when lifetime productivity of the cow is optimized. To achieve this goal, heifers must calve early in the season as 2-yr olds (Lesmeister et al. 1973; Marshall et al. 1990) and this requires pregnancy establishment by 15 mo of age. Recognition of an inverse relationship between body weight and age at puberty (Schillo et al. 1992) led to the concept of nutritional management for heifers to achieve 61% to 65% of mature body weight at first breeding (Goehring 1991). However, pregnancy rate has been 21% higher in heifers when first service was at the third rather than first estrus of the breeding season (Byerley et al. 1987). Prior to the third estrus, there is a greater frequency of abnormal cycle length and ovarian/uterine endocrine function (Del Vecchio et al. 1992). Therefore, management of heifers has emphasized

early attainment of puberty, which may be influenced by many environmental (social and climatic), nutritional and genetic factors (Vandenbergh 1989; Martin et al. 1992; Small et al. 2000). Faster-gaining heifers reach puberty earlier than slower-gaining heifers, but the consequences of over- or under-feeding are negative for fertility and milk production (Short and Bellows 1971; Patterson et al. 1992).

Photoperiod has long been recognized as one of the multitude of environmental stimuli responsible for the seasonal effects on reproductive function in cattle (Hansen 1985). Earlier studies, in which lighting conditions were often

Abbreviations: EP, extended photoperiod; IGF-I, insulin-like growth factor I; LH, luteinizing hormone; NP, natural photoperiod; P, photoperiod; T, time

incompletely described, or incompatible with practical implementation, produced inconsistent effects on heifer development. Puberty occurred earlier (Petitclerc et al. 1983) or at a younger age and body weight (Ringuet et al. 1994) when indoor-housed Holstein heifers were provided with a long (16 h) rather than short (8 h) photoperiod. Long photoperiod has also been shown to stimulate growth (Peters et al. 1980; Zinn et al. 1986a) and enhance deposition of lean tissue (Petitclerc et al. 1984) with (Peters et al. 1980) or without (Peters and Tucker 1978) increased feed consumption. Other studies reported that long photoperiod had no effect (Petitclerc et al. 1984; Phillips et al. 1997) or reduced growth rate (Zinn et al. 1986b), or reduced fat deposition (Phillips et al. 1997).

Prolactin secretion by the posterior pituitary responds to gradual increases and decreases in daylength (Crister et al. 1988). Prolactin has also been shown to increase in ovariectomized beef heifers exposed to supplemental light provided in a confinement area after animals had been exposed to natural photoperiod outdoors (Crister et al. 1987). Other studies have shown long photoperiod to increase (Bourne and Tucker 1975; Petitclerc et al. 1983) or have no effect on prolactin in cattle (Peters et al. 1980; Petitclerc et al. 1984; Phillips et al. 1997). Others suggest that the absence of an effect of photoperiod on prolactin may be due to cold ambient temperature (-10 to 6°C ; Peters et al. 1980; Zinn et al. 1986b).

Photoperiod manipulation has not been considered a significant management tool for cattle as it has for seasonal breeders like sheep. Clearly there is some controversy over the effects of photoperiod on prolactin, growth and development of cattle. In all studies except Phillips et al. (1997), the effects of photoperiod were examined in the absence of all the elements of weather. In western Canada, the majority of calves are born in the spring, and postweaning growth occurs in winter, and cattle are typically housed outdoors. Given that the lower critical temperature for growing cattle is believed to be -19°C (Webster 1970), and maintenance requirements may increase as much as 40% during chronic cold exposure [National Research Council (NRC) 1996], it was of interest to determine if supplemental light would overcome negative effects of winter on growth performance and hence the onset of puberty.

The objective of this study was to determine the effects of extending the winter and early spring photoperiod using a practical, clearly defined lighting system on the development of beef heifers housed outdoors in winter. The effects on puberty, growth, backfat, and prolactin in serum were examined.

MATERIALS AND METHODS

Animal Management and Treatments

One hundred and forty-four crossbred heifers were used in this study, conducted at the Agriculture and Agri-Food Canada Research Centre, Brandon, MB ($99^{\circ}57'03''\text{W}$; $49^{\circ}54'35''\text{N}$; 367 m elevation). The heifers, born March–April, were progeny of Continental (Gelbvieh, $n = 64$, Simmental, $n = 30$), British (Red Angus, $n = 39$, Hereford, $n = 8$) and Composite (1/4 Simmental, 1/4 Charolais, 1/16 Limousin, 7/16 British, $n = 3$) sire breeds and either 1/2

Simmental \times 1/2 Hereford, 1/2 Simmental \times 1/2 Red Angus, or Composite dams. All animals were cared for in accordance with the guidelines of the Canadian Council on Animal Care (1993).

At weaning, in autumn (5 October 1998), heifers were assigned by body weight and sire breed to one of two similar open shed/drylot housing facilities that were equipped to provide one of two photoperiod treatments (EP = extended photoperiod and NP = natural photoperiod). Body weight and age at weaning were 225 ± 23 kg and 187 ± 14 d (mean \pm standard deviation), respectively. All heifers were exposed to natural photoperiod before and after the EP treatment of 16 h (natural + supplemental light) was applied. The EP treatment was gradually introduced over 3 wk by lengthening photoperiod by 2 h once weekly from 8.4 h on 1 December 1998 to 16 h by the time of the winter solstice (21 December = 0 wk) and continuing at 16 h until 10 May 1999 (20 wk). Natural daylight during this time decreased from 12.2 h at the autumn equinox to 8.1 h on 21 December and increased to 15.2 h on 10 May.

Two timers controlled the lights, with one timer (EL71/120 Single Channel Controller, Paragon Electric Company, Inc., ON, Canada) controlling the on/off function and the other (Logo 230R, Siemens, Winnipeg, MB, Canada) controlling the dusk simulation. The EL71/120 timer contained an "Astro" feature that adjusted the on time of the lights each day, based on the latitude of Brandon. The lights came on 30 min before sunset so that EP animals did not experience a natural sunset before the beginning of supplemental light. At the end of the 16-h photoperiod, dusk was simulated by staggering shut-down of the lights at 5-min intervals over a 30-min period giving a total of 16.5 h of light.

The lighting was designed to achieve an intensity of 400 lx at 1 m above ground (approximately animal eye level). The design used three types of luminaries (floodlights, roadway luminaires and sentinels), all using high-pressure sodium clear lamps that have a color rendition index (CRI), of 50 on a scale of 1–100, with 100 being the greatest degree of whiteness (Chastain and Hiatt 1998). The intensity of light was measured in November and March. Readings were taken with the light meter (Optikon Litemate III, PhotoResearch, Kitchener, ON, Canada) in both a horizontal and vertical orientation at 1 m above ground at each point on a predetermined grid (20 points per pen).

The facility for the NP treatment had no light sources within the shed or drylot, and was free from spill-over light from surrounding buildings, resulting in an environment of darkness following natural sunset. The facilities for EP and NP treatments were separated by approximately 500 m. Each facility was divided into two pens to accommodate feeding and handling of the heifers. Both facilities consisted of a southern exposed straw-bedded shed (7.6 m² and 5.6 m² per heifer for EP and NP treatments, respectively) on the northern end of a drylot, with concrete feed bunks (101 cm per heifer) at the southern end of the lot. Both facilities met the recommended space requirements for this class of livestock and type of housing facility (Alberta Agriculture, Food and Rural Development 1995).

Table 1. Average daily amount of mixed ration offered to spring-born beef heifers between weeks when body weights were measured (0 wk = 16 h extended or natural photoperiod treatments), the proportion of ingredients in the ration dry matter and nutrient composition of ingredients

Period (target)	Dry matter (kg d ⁻¹) ± SD	Ingredients of mixed ration			
		Alfalfa- brome hay ^z	Barley silage ^z	Steam rolled barley ^y	Pellet ^x
			<i>Proportion of dry matter (%)</i>		
-6 to -2 wk (adjustment)	5.7 ± 0.5	60.5	39.5	0.0	0.0
-2 to 6 wk (low gain)	7.3 ± 0.7	65.2	34.8	0.0	0.0
6 to 10 wk (adjustment)	8.6 ± 0.5	14.0	47.6	19.1	19.3
10 to 18 wk (high gain)	10.5 ± 0.7	12.7	51.5	18.1	17.6
			<i>Nutrient composition per kg ingredient dry matter</i>		
Dry matter (g)		849	394	882	902
Digestible energy (MJ)		10.0	12.2	15.5	13.7
Crude protein (g)		175	124	139	100
Acid detergent fiber (g)		400	346	79	NA ^w
Calcium (g)		13.1	3.9	0.6	5.9
Phosphorus (g)		2.3	2.7	3.9	8.5
Magnesium (g)		2.3	1.8	1.3	4.1
Potassium (g)		23.8	18.9	5.0	7.8
Chloride (g)		4.9	3.6	1.8	NA
Sulfur (g)		2.7	3.5	1.6	2.1
Copper (mg)		4.0	4.0	4.1	NA
Molybdenum (mg)		0.5	1.0	0.7	NA
Manganese (mg)		55.8	23.7	18.3	NA
Zinc (mg)		14.3	16.7	31.0	NA

^zValues for hay and silage are based on laboratory analysis of samples taken at the time of conservation.

^ySteam-rolled barley introduced at 5 wk.

^xThe pelleted supplement, introduced at 6 wk, contained per Mt crushed barley (941.3 kg), mineral mix (28 kg containing Se 0.025, Ca 155, P 155, Mg 20, Na 0.2 I 0.2, Fe 5.0, Cu 4.0, Mn 5.0, Co 0.05, Zn 10, F 2 g kg⁻¹, and vitamins A 500, D₃ 55, E 0.5 KIU kg⁻¹), cobalt-iodized salt (10 kg), strong ADE (0.7 kg containing A 10 000 000, D 1 000 000, E 100 000 IU kg⁻¹) and limestone (20 kg).

^wNA, not analyzed.

Rations (Table 1) were formulated according to NRC (1996) to achieve pre-breeding weight (18 wk; 380 kg i.e., 60% mature weight) by a two-step rate of body weight gain; low gain (0.6 kg d⁻¹) from -2 wk to 6 wk, then over the next 4 wk gradual introduction to a ration for high gain (1.2 kg d⁻¹) from 10 to 18 wk. For low gain, heifers were offered a 100% forage ration consisting of a mix of barley silage and chopped alfalfa/brome hay (48% dry matter, digestible energy 11.4 MJ kg⁻¹ and crude protein 142 g kg⁻¹) and trace-mineral salt free choice. For high gain, heifers were gradually stepped-up to a 64% forage:36% concentrate mixed ration consisting of barley silage, chopped alfalfa/brome hay, steam-rolled barley and a pelleted supplement (54% dry matter, digestible energy 12.8 MJ kg⁻¹ and crude protein 129 g kg⁻¹). During both periods, feed was offered (Table 1) once daily by experienced staff who visually scored the amount of feed in the bunks just before feeding, and adjusted the amount of feed offered, up or down 0.5 kg per animal, to maintain 10% feed refused (orts). Adjustments were made equally for both treatment groups so that each received the same amount of feed at all times. The amount of feed and number of animals per pen were recorded daily.

Estrus Detection

Visual observations for behavioral estrus (standing heat) were performed in the morning and evening, for a minimum of 20 min at each facility, each time. The timing of estrus detection was adjusted to coincide with natural sunrise and

sunset. Detection times were 0830 and 1600 from -5 to 5 wk, 0800 and 1700 from 5 to 13 wk and 0700 and 1900 from 13 to 21 wk. Estrus with ovulation (puberty) was confirmed by analysis of progesterone in blood serum collected 8 to 12 d after the estrus observation. Progesterone greater than or equal to 1.0 ng mL⁻¹ was considered indicative of a functional corpus luteum, and less than 1.0 ng mL⁻¹ indicative of the absence of a functional corpus luteum (Small et al. 2000). Length of the estrous cycle was calculated as days between confirmed estruses.

Sampling and Hormone Analysis

Body weight, backfat measurements and a blood sample for serum prolactin analysis were taken every 28 d beginning at -6 wk. On three occasions (-6, -2 and 18 wk) body weights were the average of weights taken on 2 consecutive days. Backfat thickness between the 12th and 13th ribs was measured using real-time ultrasonography (Aloka SSD500, 5.0 Mhz probe, Aloka Co. Ltd., Japan) every 28 d beginning at -2 wk.

Blood samples were collected by caudal venipuncture using 10-mL non-heparinized evacuated tubes and 20-gauge, 1" multi-draw needles. Serum harvested after centrifugation (1000 × g for 40 min at 4°C) was transferred into labeled tubes and stored frozen (-20°C) until further analysis. Serum progesterone concentrations were determined by an established enzyme-immunoassay, which had a detection limit of 0.03 ng mL⁻¹ (Del Vecchio et al. 1995). The coefficients of variation within and between ($n = 11$) assays were 6.7 and 10.2%, respectively. Prolactin concentrations were

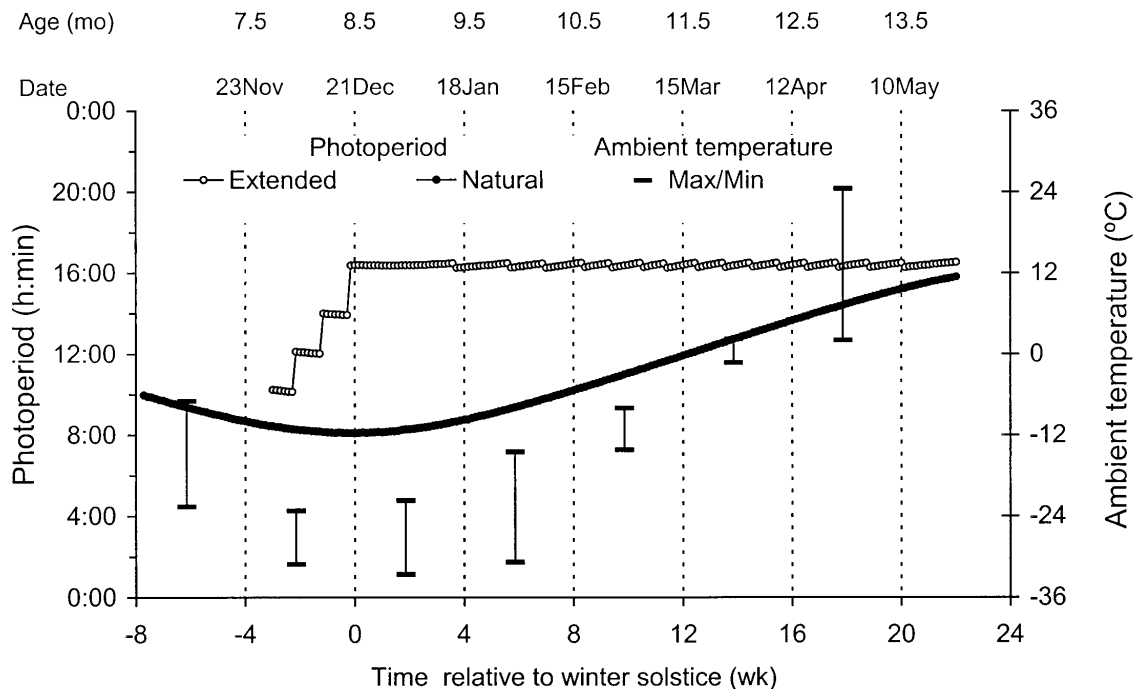


Fig. 1. Duration of autumn, winter and spring light exposure for heifers assigned at weaning (-8 wk) to extended (0 wk = 16 h light) and natural photoperiod treatments in winter and spring, and ambient temperature maxima and minima on the days of blood sampling for prolactin analysis.

determined by a double-antibody radioimmunoassay at the Western College of Veterinary Medicine, University of Saskatchewan, Saskatoon, SK. Assay sensitivity was 0.5 ng mL^{-1} and coefficients of variation within and between ($n = 7$) assays were 8.0 and 9.9% , respectively.

Weather Data and Statistical Analysis

Daily maximum and minimum temperatures and precipitation (rain and snowfall) have been recorded at the Brandon Research Centre since 1890. Data for the experimental period were extracted from the database and compared to the monthly average temperatures, precipitation and frequency of precipitation for the previous 30 yr.

Statistical analyses of the data were performed using the SAS Institute Inc. v 6.12 (SAS Institute, Inc. 1996). Body weight, backfat and prolactin data were analyzed using the general linear models procedure with repeated measures and type III sums of squares separately for the low gain (-2 to 6 wk) and high gain periods (10 to 18 wk) since times from -6 to -2 wk and from 6 to 10 wk were considered periods of adjustment to changes in the ration. Sources of variation in the final analysis included photoperiod (P), time (T), and the interaction ($P \times T$), using animal within photoperiod treatment as the error term for P ($df = 142$) and residual as the error term for T and ($P \times T$) ($df = 284$). Average daily gain in body weight for the low and high gain periods were determined by regression and analyzed by one-way analysis of variance ($df = 142$). Initial statistical analysis showed no significant ($P > 0.05$) effects of breed or pen which were therefore excluded from the final model. The cumulative proportion of heifers having one,

two, or three confirmed estruses at weekly intervals were compared between NP and EP using the Categorical models (CATMOD) procedure for chi-square analysis. Paired t -tests were used to compare weather data for the study period with the previous 30-yr average.

Values are expressed as the mean \pm the pooled standard error unless otherwise stated and as standard deviation for data not subjected to analysis of variance. Significance was set at $P < 0.05$.

RESULTS

The intensity of supplemental lighting was 480 lx horizontally and 380 lx vertically in November and 504 lx horizontally and 328 lx vertically in March. During this study, ambient temperatures were similar ($P > 0.05$) to the 30-yr average for winter (November to March; $-12.2 \pm 6.6^\circ\text{C}$) and spring (March to June; $4.2 \pm 5.1^\circ\text{C}$); however there were fewer days with snowfall (29 vs. 42.5 d $P < 0.05$) but similar total snow in winter (96.4 vs. 68.3 cm; $P > 0.05$). During the winter months there were 50 d when the minimum temperature was below -20°C and 98 d when the maximum temperature was below 0°C . In spring there were 2 d when the maximum temperature was below 0°C and 15 d when the maximum temperature was above 20°C . The duration of the photoperiod for the EP and NP treatments, and ambient temperature minima and maxima on the days of blood sampling for prolactin is shown in Fig. 1.

Puberty and Pubescent Estrous Cycles

Photoperiod influenced ($P < 0.05$) the cumulative proportion of heifers that attained puberty by 20 wk (Fig. 2), but did not

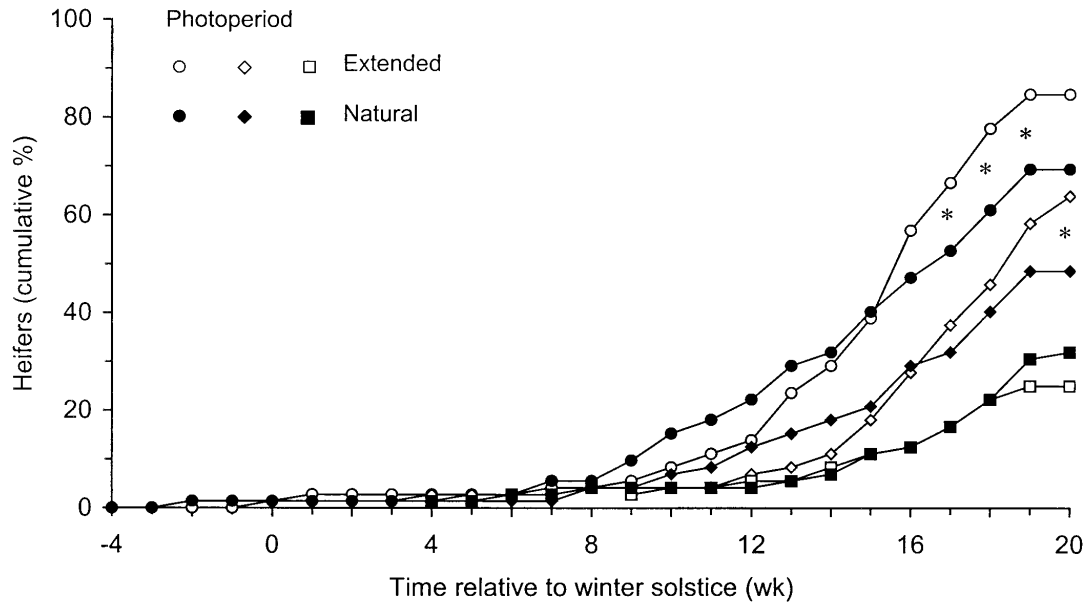


Fig. 2. The cumulative proportion of heifers, exposed post-weaning to extended ($n = 72$, 0 wk = 16 h light) or natural photoperiod ($n = 72$) treatments in winter and spring, that exhibited one (\circ , \bullet), two (\diamond , \blacklozenge) or three (\blacksquare , \square) progesterone confirmed estruses by yearling age. * Proportions within estrus groups are different between photoperiod treatments ($P < 0.06$).

influence ($P > 0.05$) the length of pubescent estrous cycles. By the end of the low gain period (6 wk) only two heifers (1.4%, $n = 144$) had attained puberty. By the beginning of the high gain period (10 wk) the proportion of animals in the EP ($n = 72$) and NP ($n = 72$) treatments that attained puberty did not differ (6.9 vs. $13.8 \pm 2.6\%$; $P > 0.05$), but by the end of the high gain period, was greatest for EP (84.7 vs. $69.4 \pm 3.1\%$; $P < 0.05$). At 20 wk, the proportion of heifers that had two estruses tended to be greater for EP than NP treatments (63.9 vs. $48.6 \pm 3.4\%$; $P = 0.06$) but three estruses did not differ (29.2 vs. $27.8 \pm 3.3\%$; $P > 0.05$). Mean cycle length (17.9 ± 1.0 d) and the proportion of abnormal length cycles in either the first or second estrous cycles did not differ ($P > 0.05$) between treatments. Overall, 59% of first and 63% of second estrous cycles were of normal length (18 to 24 d) and the majority of abnormal length cycles were due to short (36%) rather than long (4%) cycles.

Body Weight, Backfat and Prolactin

Body weight and backfat were influenced by the interaction of photoperiod with time ($P < 0.05$) during the low gain period and by time ($P < 0.05$) during the high gain period (Fig. 3). During the low gain period, the rate of body weight gain was greater ($P < 0.05$) for EP than NP treatments (0.59 vs. 0.52 ± 0.01 kg d^{-1}) while the rate of ultrasonically estimated backfat gain was lower ($P < 0.05$) for EP than NP treatments (0.017 vs. 0.020 ± 0.001 mm d^{-1}). During the high gain period, the rate of gain in body weight and backfat did not differ between EP and NP treatments (1.32 vs. 1.27 ± 0.03 kg d^{-1} and 0.037 vs. 0.039 ± 0.03 mm d^{-1} , respectively). Based on feed offered, daily intake of digestible energy and crude protein (mean \pm standard deviation) were approximately 83 ± 10 MJ and 1.02 ± 0.06 kg during the low gain period and 134 ± 9 MJ and 1.35 ± 0.09

kg during the high gain period, respectively, for both treatment groups.

Serum prolactin was influenced by the interaction of photoperiod with time ($P < 0.05$) during the low gain period and by time ($P < 0.05$) during the high gain period (Fig. 4). Prolactin was less than 6 ng mL^{-1} for NP from -2 wk to 6 wk, but twice this level for the EP treatment at 2 wk and 6 wk. During the high gain period prolactin increased for both treatments from approximately 15 ng mL^{-1} at 10 wk to 136 ng mL^{-1} at 18 wk.

DISCUSSION

This study has shown that management of photoperiod influences the growth and reproductive function of beef heifers housed outdoors in a prairie winter environment. The arrangement of high-pressure sodium lamps on timers, in a typical open shed/lot facility, provided supplemental light (400 lx), beginning 1/2 h before sunset, to extend the winter and early spring photoperiod to 16 h (EP) at a time when heifers in a similar facility without lighting (NP) were exposed to only natural photoperiod that gradually increased from 8 h (0 wk) to 15 h (20 wk). The effects of photoperiod on growth and backfat were not due to an increase in feed intake because the amount of dry matter offered daily was the same for both treatment groups. This indicates that photoperiod, perhaps through its effect on prolactin or other light-sensitive hormones, influenced nutrient partitioning for lean growth. The effect of photoperiod on puberty was not due to differences in body weight or condition (backfat), that did not differ between treatment groups at this time, indicating that the effect of photoperiod was additive to the effect of a change from a low (83 MJ d^{-1}) to a high (134 MJ d^{-1}) energy intake (flushing) and perhaps advancing age on ovarian function.

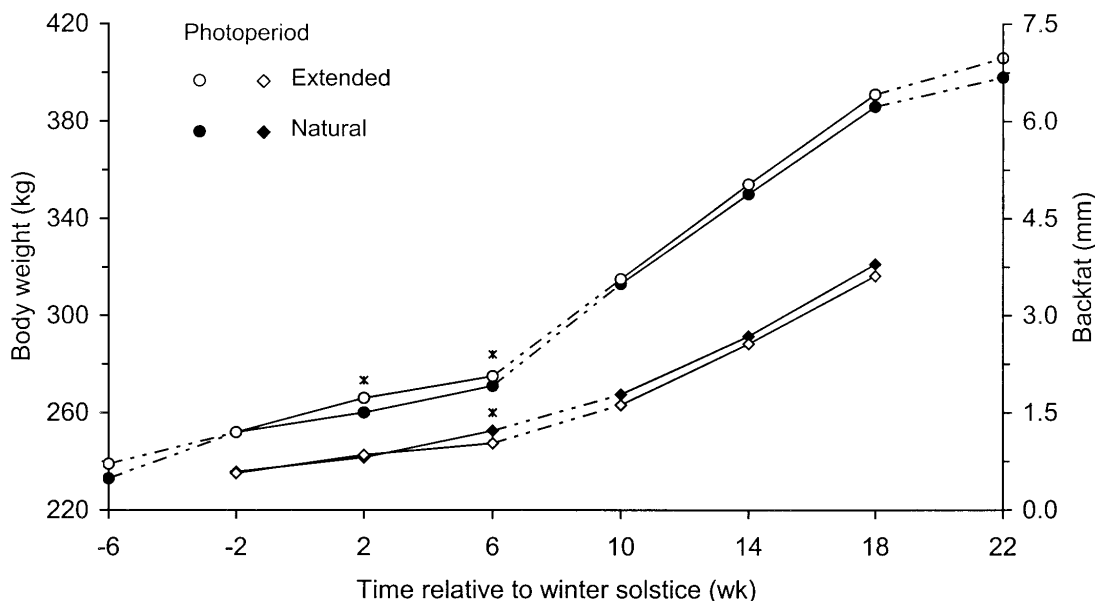


Fig. 3. Mean body weight (\circ , \bullet) and backfat (\diamond , \blacklozenge) of heifers exposed post-weaning to extended (0 wk = 16 h light) or natural photoperiod treatments in winter and spring. Photoperiod \times time interaction was significant ($P < 0.05$) for body weight (SE = 0.46) and backfat (SE = 0.04) during the low gain period (-2 to 6 wk; df = 284), but not ($P > 0.05$) during the high gain period (10 to 18 wk df = 284), when the SE body weight and backfat were 0.7 and 0.06. * Points in time when change from -2 wk differs ($P < 0.05$) between treatments. Dashed lines represent ration adjustment periods.

Lighting Conditions

The mean intensity of supplemental light in this study was higher than that used by many others, but similar to that used in an outdoor study by Phillips et al. (1997). Light intensities between 200 and 600 lx increase prolactin secretion in cattle (Tucker et al. 1984; Crister et al. 1987), and a minimum intensity of 100 lx, but ideally 200 lx, is recommended to improve milk production of dairy cows (Chastain and Hiatt 1998). However, it is not known whether this management recommendation influences reproductive function. Although spectral properties of different lamps (incandescent, high pressure sodium, and mercury vapor) did not influence the increased prolactin response to long photoperiod in bulls (Stanisiewski et al. 1984), it is not known if the spectral properties of light affects heifers or influences the response to photoperiod treatments applied in an outdoor environment.

Growth and Backfat

The rate of body weight gain was approximately 14% higher and backfat accumulation 22% less for EP than the NP treatments during the low gain period when heifers were prepubescent, but did not affect growth when heifers were pubescent and fed for a high rate of body weight gain. Increased feed intake has been associated with increased growth rate in response to long photoperiod (Peters et al. 1980), but in our study feed intake was not a factor. The daily dry matter offered was the same for both groups at all times; approximately 2.8% of body weight. Our results agree with other results, that a growth response to extended photoperiod is not necessarily associated with increased feed intake in heifers (Enright et al. 1995; Phillips et al.

1997). An effect on weight gain and backfat without affecting feed intake indicates our supplemental light treatment influenced the composition of body weight gain (nutrient partitioning), likely promoting lean growth prior to puberty.

A small weight gain advantage with extended photoperiod for prepubescent heifers has been reported by others (Peters et al. 1980; Petitclerc et al. 1983; Zinn et al. 1986a; Enright et al. 1995). The advantage in weight gain tended to be greater with 3, 4, or 8 h of additional light at a light intensity of 600 lx and one or two dark phases, than 8 h at 300 lx and one dark phase (Enright et al. 1995), and in contrast to our study, not associated with any differences in backfat (Zinn et al. 1986b; Enright et al. 1995). Our results are in contrast to those of Phillips et al. (1997) where 400 lx did not increase weight gain in prepubescent heifers, but in agreement in that extended photoperiod reduced subcutaneous fat accumulation. However, post-puberty, supplemental light did not affect weight gain or reduce subcutaneous fat accumulation in our study and others (Enright et al. 1995; Phillips et al. 1997). Yearling steers, but not postpubescent heifers, showed transient effects on weight gain within the first 2 wk of supplemental light treatment, that was subsequently compensated for, but resulted in carcasses that had less fat than steers exposed to natural photoperiod (Phillips et al. 1997). Therefore, the results of our study and others are similar in that the composition of weight gain is influenced by photoperiod, and the effects are different depending upon reproductive function, but differ on whether or not the effect is on lean or fat tissue growth. Our results show that the effect of photoperiod on gain in body weight and backfat was different at low- and high-energy intake. Furthermore, in our 20-wk

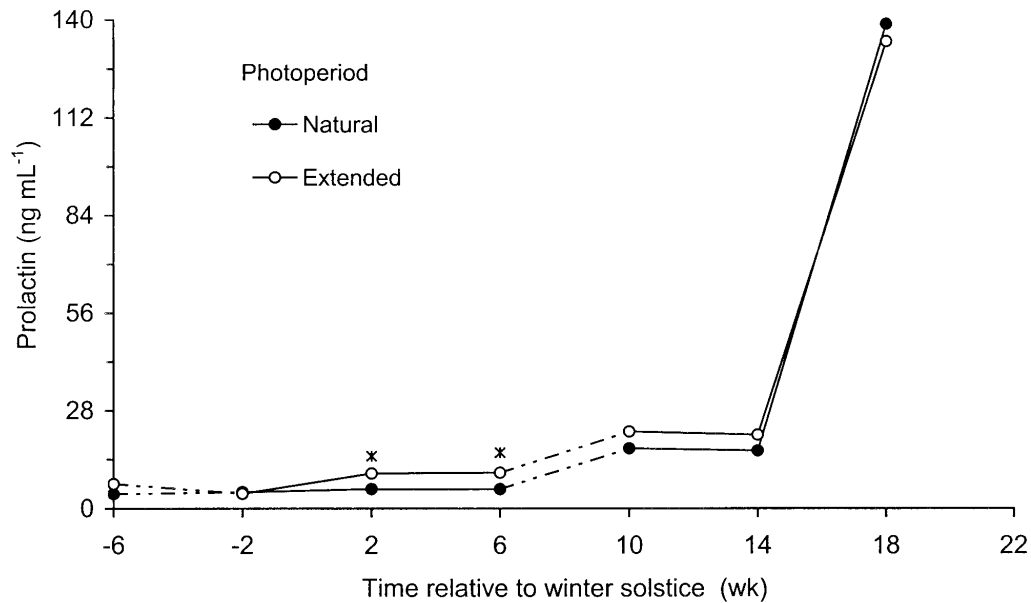


Fig. 4. Mean serum prolactin concentrations in heifers exposed post-weaning to extended (0 wk = 16 h light) or natural photoperiod treatments in winter and spring. Photoperiod \times time interaction was significant ($P < 0.05$) during the low gain period (-2 to 6 wk; $SE = 1.07$ $df = 284$), but not ($P > 0.05$) during the high gain period (10 to 18 wk; $SE = 10.0$ $df = 284$). * Points in time when change from -2 wk differs ($P < 0.05$) between treatments. Dashed lines represent ration adjustment periods.

study, there were 7 wk with ambient temperature minima below -20°C ; no doubt the animals became acclimated to cold, which may have influenced the effect that cold would have on fattening. Given that the lower critical temperature for growing cattle is -19°C (Webster 1970), it is unlikely that cattle were “cold” exposed in studies that reported a mean ambient temperature of 3.5°C in November (Phillips et al. 1997) or a range from -10°C to 6°C (Peters et al. 1980; Zinn et al. 1986b). The inconsistency in the literature with respect to the effect of extended photoperiod on weight gain and the composition of gain may be due to energy intake and/or interaction between energy intake and reproductive function and/or ambient temperature.

Feeding level and photoperiod influence lipid metabolism and nutrient partitioning between adipose tissue and muscle in ruminants, in part, by modulation of lipogenic enzymes and lipoprotein lipase gene expression (Faulconnier et al. 1999). In the ovariectomized ewe, the effect of photoperiod on lipogenic activity of adipose tissue and lipoprotein lipase activity of muscle is independent of nutrient availability (Faulconnier et al. 2001). Sheep are typically short day breeders and at this time lipid mobilization would be expected to be a positive activity for reproductive function. Seasonality of reproductive function is not as strong in cattle as it is in sheep, but typically beef cattle in Canada are managed for breeding in the early spring when daylength is increasing (Small and McCaughey 1999), and in winter fed to allow little or no reduction of the backfat accumulated over the summer (Richards et al. 1986; NRC 1996). The seasonality of lipid metabolism in the ewe may be similar in mature cattle, but spring-born heifers accumulate fat during their first winter so it may be that sensitivity to photoperiod

has not developed or is reversed at this stage such that limiting the exposure to short days or long photoperiod delayed fat accumulation.

Puberty and Pubescent Estrous Cycles

Extended photoperiod resulted in a 22% improvement in the number of heifers that reached puberty as yearlings and a 31% improvement in the number having a second confirmed estrus. Previous studies have reported stimulatory effects of long photoperiods on puberty in beef (Hansen et al. 1983; Enright et al. 1995) and dairy (Petitclerc et al. 1983; Ringuet et al. 1994) heifers. This relationship was of particular interest in the present study, the first to be conducted outdoors under winter conditions typical of the Canadian beef industry.

The onset of puberty may be triggered by attainment of a critical body weight, and is dependent on development of endocrine function during the prepubescent period (Schillo et al. 1992; Del Vecchio et al. 1992). In our study, a greater proportion of EP animals achieved puberty as yearlings when weight gain was high and body weight and fatness not different from NP animals, indicating that the influence of photoperiod was additive to the effects of a high-energy ration and perhaps advancing age on ovarian function. As with our study, older literature did not show a consistent relationship between puberty and level of body fatness (Schillo et al. 1992). This may be because leptin, a hormone secreted by adipose tissue, rather than specific fatness, informs the central nervous system of fat reserves and “fatness” to trigger puberty in sheep and cattle (Chilliard et al. 1999). In sheep, leptin is sensitive to photoperiod, increasing with increasing daylength (Chilliard et al. 1999).

During the prepubescent period, the increasing frequency of the pulsed release of luteinizing hormone (LH), stimulating follicular development and decreasing sensitivity of the pituitary to the negative feedback of estradiol, is a key prerequisite of puberty (Schillo et al. 1992). In our study, puberty did not occur in 99.6% of heifers until adjustment to the high gain ration. Moderate energy restriction suppresses LH pulse frequency (Day et al. 1986), whereas a high energy intake increases the frequency of LH pulses such that puberty occurs at a younger age, but the same body weight as heifers fed a lower energy ration (Hall et al. 1994). Heifers on a high plane of nutrition have higher concentrations of insulin-like growth factor I (IGF-I) and insulin (Yelich et al. 1996; Armstrong et al. 2001), that are stimulatory to LH release (Schillo et al. 1992) and mean plasma IGF-I is positively correlated with average daily gain in heifers (Auchtung et al. 2001). It has been proposed that the effect of high energy intake on insulin and IGF-I influences the rate of follicular growth by increasing ovarian sensitivity to follicle stimulating hormone (Armstrong et al. 2001). It is likely that insulin and IGF-1 increased when the ration was changed to high energy, but other factors must have been involved to explain the additive effect of photoperiod. This may have been a consequence of the effect of photoperiod on growth during the prepubescent period, or a direct effect of photoperiod during pubescence or a combination of these factors.

Growth hormone and leptin have also been identified in the endocrine processes leading to puberty in cattle. In grazing heifers insulin and growth hormone did not change throughout growth and prepubescence, but leptin was correlated with body weight and a surge occurred 2 wk prior to a rise in progesterone (puberty) (Diaz-Torga et al. 2001). In heifers given conserved feed, plasma growth hormone was not influenced by the energy level of the diet, but dropped 30 to 40% at 1 wk before puberty (Yelich et al. 1996). In vitro, stimulation of leptin production by glucocorticoids and insulin is inhibited by growth hormone (Chillard et al. 1999). Given that growth hormone has a seasonal secretory profile (Borromeo et al. 1995) and leptin is influenced by photoperiod (Faulconnier et al. 1999) more knowledge in this area may prove to be of significance for developing management strategies that use supplemental light to improve production efficiency of cattle.

The proportion of abnormal pubescent estrous cycles did not differ between EP and NP treatments and therefore photoperiod influenced the processes leading up to puberty, but the final stages of sexual maturation for regular length estrous cycles must be coordinated through events following puberty, that are possibly unrelated to photoperiod. Approximately 40% of first estrous cycles, and 35% of second estrous cycles were of abnormal length, and the majority of abnormalities were due to short cycles. Short cycles are indicative of improper development of the corpus luteum, and asynchrony in the endocrine function of the hypothalamic-pituitary-ovarian-uterine pathway (Del Vecchio et al. 1992). Long cycles accounted for a smaller proportion of abnormalities in the length of the first two estrous cycles and were likely due to silent estrus; the occur-

rence of ovulation without the expression of behavioral estrus (Del Vecchio et al. 1992).

Prolactin

Prolactin was twofold greater for the EP than the NP treatments in winter (2 to 6 wk) when serum prolactin is typically at the lowest concentrations in cattle (Peters and Tucker 1978; Berardinelli et al. 1992; Cho et al. 1998). Thereafter, the seasonal change in serum prolactin was similar between groups and increased 30-fold with the transition from winter (December) to spring (May). In beef heifers, the correlation coefficients are high between seasonal concentrations of prolactin and the duration of daylight, and the average minimum and maximum temperatures, and concentrations in spring have been as much as 60-fold greater than winter (Cho et al. 1998).

Older literature suggests that the effect of photoperiod on prolactin may be dependent upon ambient temperature on the day of sampling, with temperatures below 0°C suppressing an increase (Peters et al. 1980; Zinn et al. 1986b). Our study does not support this hypothesis, as an increase in prolactin was measured in months when the average temperature was below 0°C and specifically the maximum ambient temperature was -21°C and -15°C at the 2 and 6 wk samplings, respectively. In the studies by Peters et al. (1980), ambient temperature, as mentioned previously, was not necessarily cold and it is more likely that the average light intensity used, approximately 100 lx, was not sufficient to cause a rise in prolactin. Other studies utilizing light intensities greater than 200 lx have reported that long photoperiod caused an increase in prolactin when ambient temperatures were around 0°C (Zinn et al. 1986b; Phillips et al. 1997). Therefore, the variation in serum prolactin observed in our study reflected normal variation in response to season, but the supplemental light treatment reduced the duration of the winter nadir of prolactin secretion, that we observed, from 8 wk to less than 4 wk. It is not known if daylength affects hormones with seasonal secretory profiles in beef cattle. Earlier work that compared fixed 16L:8D and 8L:16D photoperiods showed an increase in prolactin and concomitant increase in mammary parenchyma tissue in dairy heifers exposed to long photoperiod (Petitclerc et al. 1985). The increase in prolactin prior to puberty observed in our study may have an effect on subsequent lactation given the role of prolactin in facilitating mammary gland development (Knight 2001).

In conclusion, our study demonstrates that manipulation of photoperiod influences the growth and reproductive function of cattle. Further research in this area will provide information needed to develop non-invasive, non-hormonal, energy-efficient management strategies using light to reduce the business risk of beef heifer development.

ACKNOWLEDGMENTS

The authors thank Dean Sykes (Senior Herdsperson), Ron Kristjansson (Junior Herdsperson) and all Beef Program staff for their assistance in conducting this research. The expertise and assistance of Paul Wasney and Ray Boris of Manitoba Hydro is gratefully acknowledged. This research was funded by Manitoba Hydro, and the Agriculture and Agri-Food Matching Investment Initiative (#A03475).

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