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Accelerated lambing achieved by a photoperiod regimen consisting of alternating 4-month sequences of long and short days applied year-round[1]

J. Cameron,* B. Malpaux,† and F. W. Castonguay*‡[2]

*Département des sciences animales, Université Laval, Québec, Canada, G1V 0A6;
†Physiologie de la Reproduction et des Comportements, Institut National de la Recherche Agronomique (INRA), Tours, 37380 Nouzilly, France; and ‡Dairy and Swine Research and Development Centre, Agriculture and Agri-Food Canada, Sherbrooke J1M 1Z3, Canada

ABSTRACT: The objective of this work was to evaluate the reproductive performance of ewes exposed to a photoperiodic regimen consisting of continuous alternating 4-mo periods of long days (LD: 16 h of light/d) and short days (SHD: 8 h of light/d) in an accelerated lambing program of 3 lambings in 2 yr. A total of 211 prolific Rideau Arcott ewes were assigned to the photoperiodic treatment, whereas 37 ewes were maintained under natural annual variation in day length (control group). Ewes under the photoperiod regimen were divided into 4 subgroups (A, B, C, D). All these groups of ewes were exposed to the same light regimen, but the LD and SHD light sequences were staggered by 2 mo to permit the evaluation of the effect of time and season of mating on performance of the ewes treated with the photoperiod. The control ewes were treated with intravaginal sponges in the out-of-season breeding periods (conventional approach). Each group of ewes was studied over 3 reproductive cycles. Two groups of rams exposed to alternating 2-mo sequences of LD and SHD were used for mating. The short mean interval between ram introduction and conception for the groups exposed to artificial photoperiod (9.4 d) confirmed the effectiveness of the treatment to induce intense sexual activity. For the 12 breeding periods studied (8 in out-of-season and 4 in sexual season), fertility rate of the ewes treated with photoperiod, mated at various times of year, was 91.6%, which is comparable with the fertility normally seen in the natural breeding season. The number of lambs born/ewe remained constant across reproductive cycles and was greater in photoperiod-treated groups (2.81 vs. 2.27 for photoperiod and control groups, respectively; $P = 0.0002$). Groups exposed to photoperiod treatment obtained better fertility rate than the control group in out-of-season breeding (91.1 vs. 76.3%; $P = 0.016$). Ewes managed under the photoperiod regimen produced 1.38 lambings/yr and 69% of them lambed 3 times in 2 yr. Overall, the ewes in the photoperiodic treatment produced annually 3.78 lambs/ewe. The reproductive performances achieved throughout the years indicate that the photoperiodic program tested, consisting of continuous alternating 4-mo periods of LD and SHD, allows control of the annual reproductive cycles in ewes.

Key words: accelerated lambing, fertility, photoperiod, productivity, seasonality, sheep

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INTRODUCTION

To improve sheep flock productivity, research has focused on developing intensive management systems to achieve more than one lambing per ewe each year. Because these kinds of programs, such as STAR (Lewis et al., 1996), require out-of-season breeding, they are more effective for breeds showing less seasonality in their reproduction. Because the alternation between long days (**LD**) and short days (**SHD**) is the main factor modulating seasonal reproduction in sheep (Legan and Karsch, 1980; Lincoln and Short, 1980), photoperiod manipulation could be used to develop a reproduc-

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[2]Corresponding author: francois.castonguay@fsaa.ulaval.ca

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tion program for intensive management systems that are effective and adapted to seasonal breeds.

Some studies have tested the use of artificial schedules of LD and SHD to induce intense sexual activity in the nonbreeding season (Williams and Ward, 1988; Chemineau et al., 1992). Others tried applying continuous alternating periods of LD and SHD to induce estrus in ewes at various times of the year (Vesely and Bowden, 1980; Hackett and Wolynetz, 1982). However, these programs showed variations or declines in the fertility rate with advancing reproductive cycles. The knowledge acquired over the years has increased our understanding of important aspects as the optimal interval between the start of SHD and estrus induction (Chemineau et al., 1988; Ravault and Thimonier, 1988) and the concept of refractoriness to photoperiod (Karsch et al., 1986), which brought new ideas for the development of an annual photoperiod program.

This study aimed 1) to assess the reproductive performance of sheep subjected to an annual photoperiod program based on alternating 4-mo sequences of LD and SHD continuously in an accelerated lambing system, 2) to examine the consistency of results over 3 reproductive cycles, 3) to evaluate the effect of season of mating on reproductive performance of the ewes treated, and 4) to compare results of ewes treated with photoperiod with those obtained with conventional management using natural mating in breeding season and hormonal treatment in nonbreeding season.

MATERIALS AND METHODS

The care and handling of the sheep used in this study conformed to the guidelines established by the Canadian Council on Animal Care (1993).

Animals

This study used 248 mature Rideau Arcott ewes, a very prolific breed developed in Canada (Shrestha and Heaney, 2003), and 12 rams: 6 Rideau Arcott, 2 Texel, 2 Suffolk, and 2 Dorset. At the beginning of the experiment, the average age of ewes was 1.7 ± 0.5 yr. Before the start of the experiment, all the animals were exposed to natural variations in day length.

Location

The experiment was carried out in a commercial flock at St-Lambert-de-Lévis, near Quebec City, Canada (46°37′35.72″ N, 71°09′22.75″ W). All the sheep were kept in total confinement. The females exposed to photoperiodic treatment were housed in 2 separated sections of the barn under artificial lighting provided by incandescent bulbs. In the first section (insulated, windowless), animals were exposed to a fixed LD sequence (16 h of light/d) with an average light intensity of 35 lx, measured at 5 points in each pen, at the eye level of a standing ewe. In the second section (insulated, windowless), the light exposure was set to provide SHD (8 h of light/d) and light intensity averaged 15 lx, measured as described previously. Because lighting schedules were held constant in each barn section, the animals had to be moved from one section to another to expose them to LD or SHD.

Ewes in the control group, raised under natural day length, were housed in an insulated barn located near the building used for the photoperiodic treatments. The barn had natural (windows) and artificial (incandescent bulbs) lighting. The lights were turned on at sunrise and off at dusk to mimic natural day length. In this section, light intensity ranged from 70 to 500 lx depending on outdoor weather conditions.

Management

All the ewes were managed in an accelerated lambing program of 3 lambings in 2 yr with mating planned every 8 mo. In the breeding period, each ram was equipped with a marking harness to monitor their libido and the estrous activity of the ewes. A ram:ewe ratio of 1:15 to 1:20 was used for the ewes under photoperiod treatment and for the control group mated during the natural breeding season. A ratio of 1:5 to 1:8 was used for ewes synchronized with intravaginal sponges.

Pregnancy status was assessed 70 to 75 d after ram introduction by abdominal ultrasound, using a real-time ultrasound device (Ultrascan50, Alliance Médicale Inc., Montreal, Canada) with a 120-mm, 3.5-MHz linear probe. Ewes still not pregnant after 2 successive mating periods were culled. Number of ewes culled for reasons other than reproductive failure (e.g., poor milk production or health problems) was recorded.

The ewes and rams were fed a ration consisting of round bale grass-legume silage (alfalfa, clover, and timothy), corn silage, dry hay (alfalfa, clover, and timothy), barley, corn, or soybean meal. The rations were formulated using OviRation 3.0 software (SoftAgro, St-Ulric, Canada) to meet the nutrient requirements of the NRC (1985) for the different physiological stages (flushing, gestation, and mid and late lactation).

Treatments

At the start of the experiment, ewes were assigned to treatments (photoperiod or control) according to their physiological status and their age (photoperiod: n = 211, 1.7 ± 0.6 yr old and control: n = 37, 1.6 ± 0.3 yr old).

The photoperiodic treatment consisted of 4 mo of LD (16 h of light/d) alternating continuously with 4 mo of SHD (8 h of light/d). To evaluate the effect of time of mating on performance of the ewes treated with the photoperiod program, ewes were divided randomly into 4 subgroups (A, B, C, D). Each group under controlled photoperiod was exposed to the same light regimen, but the LD and SHD sequences were staggered by 2 mo to spread mating periods throughout the year

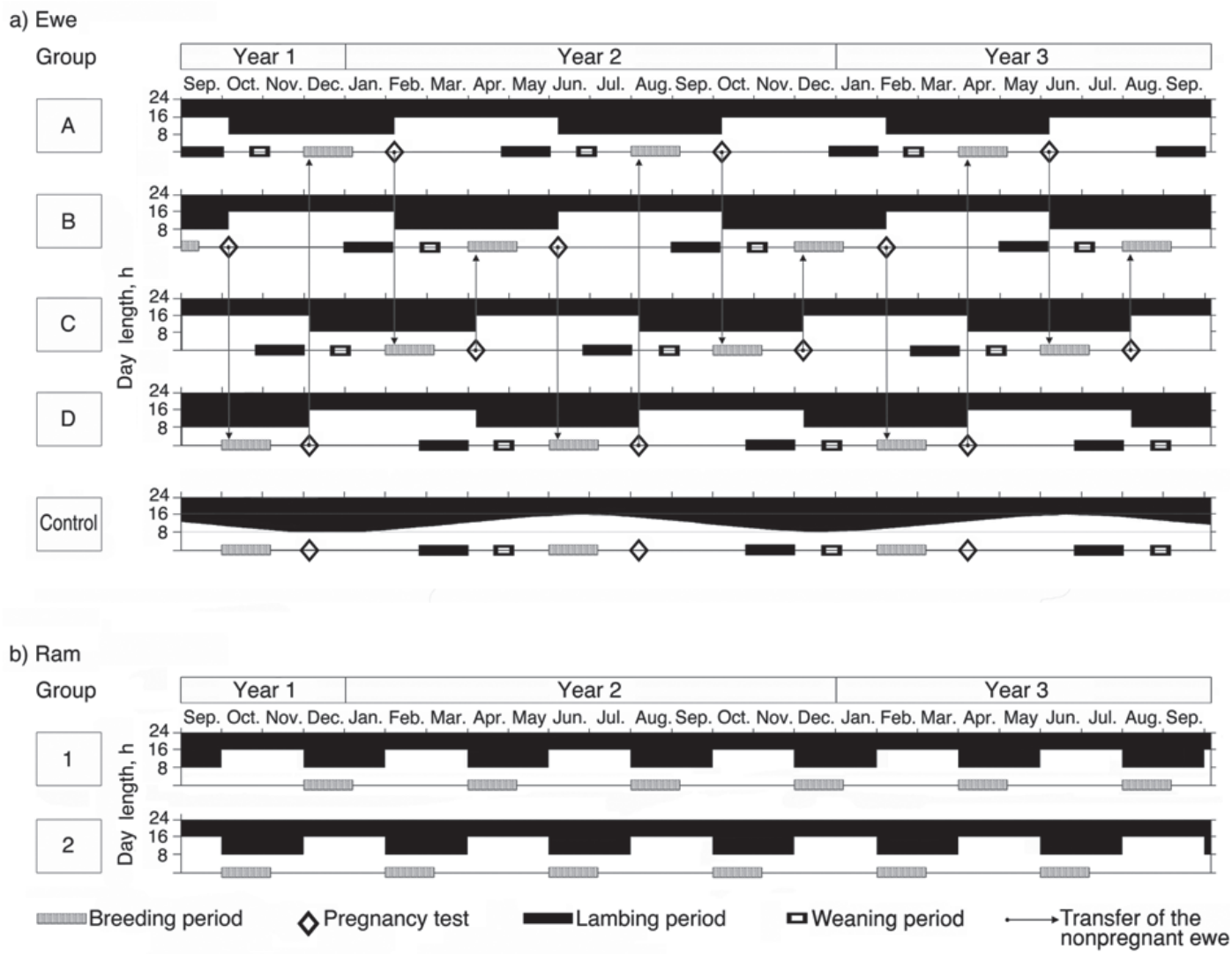

Figure 1. Management protocol of a) the 4 groups of ewes (A, B, C, and D) treated with a photoperiod regimen alternating 4 mo of long days (LD: 16 h of light/d) and 4 mo of short days (SHD: 8 h of light/d), and the control group treated with vaginal sponges in out-of-season breeding period; b) the 2 groups of rams treated with a light regimen alternating 2 mo of LD and 2 mo of SHD.

(Figure 1). The duration of the photoperiod sequences was fixed at 120 d because the development of refractoriness to the same and constant photoperiodic signal (SHD or LD) was expected to occur after 100 to 150 d of exposure to constant day length (Karsch et al., 1986; Malpaux et al., 1988b; Bocquier et al., 1997). Based on previous study by Chemineau et al. (1988) reporting that sequences of 3 mo of LD and SHD stimulates estrous activity about 50 d after the transition to SHD, the breeding period began 55 d after the start of the SHD for a duration of 35 d. In a view of practical application of the photoperiod schedule in an accelerated lambing system, and to reduce unproductive period, nonpregnant ewes at ultrasound scanning were treated with an intravaginal progestagen sponge (Veramix, Upjohn, Orangeville, Canada) for 14 d. At sponge withdrawal, ewes were injected with 450 IU of eCG (Folligon, Intervet, Whitby, Canada), transferred in SHD and introduced, 48 h later, in the following photoperiod group in mating (transfer of these ewes is represented by arrows in Figure 1). For example, at the ultrasound scanning of group A2 in October, nonpregnant ewes were treated with intravaginal sponges and transferred 16 d later to group C2, which was already in mating. Ewes transferred that way were culled if nonpregnant at the next ultrasound. When pregnant after sponge treatment, these ewes remained in their new group for the subsequent mating periods (n = 9 for the 2-yr experiment; 2 in A2 and 7 in C3).

The control group of ewes was maintained under natural lighting conditions and managed in an accelerated production system using the most conventional management protocol used in Canada and many countries in Europe. Specifically, ewes were mated naturally during the breeding season, whereas in the nonbreeding season they were treated with intravaginal sponges (14 d; Veramix, Upjohn) and eCG (450 IU at sponge withdrawal; Folligon, Intervet). Rams were placed with the ewes 48 h after sponge removal for 35 d. Nonpregnant ewes after the first breeding period (cycle 1), identi-

fied at the ultrasound scanning, were left in the control group until the next mating, whereas nonpregnant ewes in cycle 2 were culled.

At the start of the experiment, rams were divided into 2 similar groups according to breed and age (age at first mating: 1.7 ± 1.2 yr). They were exposed to a photoperiod regimen (Figure 1) consisting of alternating 2-mo sequences of LD and SHD. This treatment allows reducing seasonal variations in sexual activity in rams (Pelletier and Almeida, 1987). At the end of an LD sequence, the rams were transferred with a group of ewes for mating in SHD. Several precautions were taken to control a potential effect of ram fertility and libido. At each breeding period, ewes were always bred in 3 to 5 subgroups (1 ram/subgroup); consequently, several rams were responsible for the fertility rate of a given group. Rams used in this study were sexually mature (>8 mo of age), had a scrotal circumference greater than 30 cm at the time of breeding, and had good libido as appraised by the use of marking harness. At the end of a 35-d breeding period, the rams remained in SHD for another 25 d to complete the 2-mo sequence.

Performance Recorded

The performance of the ewes was assessed over 3 reproductive cycles. For each breeding group, the lambing rate (number of ewes lambing/number of ewes exposed to rams, excluding ewes that died during gestation) and prolificacy (number of lambs born/number of ewes lambing) were calculated. The birth weights of the lambs were recorded. The date of conception was estimated by subtracting 145 d (approximate gestation duration) from the date of lambing. The ewe culling rate was calculated for each reproductive cycle (number of ewes dead or culled/number of ewes exposed to rams). Body condition score (1 to 5; 1 being an emaciated sheep) was assessed at the time of breeding (ram introduction), at ultrasound pregnancy testing, 5 wk before lambing, and at lambing. Annual productivity was calculated as the total number of lambings during the 2-yr period divided by the mean number of ewes in a given treatment during the 2-yr period, divided by 2 yr.

Progesterone and Melatonin Profiles

Progesterone concentration was assessed in a subgroup of 20 ewes under photoperiod treatment (group D at second mating) to determine the onset of estrous cycle after the beginning of SHD. Blood samples were taken twice weekly, beginning 31 d and ending 84 d after the start of SHD. The samples were collected by jugular venipuncture into 10-mL Vacutainer heparin tubes (Becton Dickinson and Co., Franklin Lakes, NJ). The tubes were placed on ice and centrifuged within 1 h (1,800 × *g* for 20 min at room temperature). The plasma was collected and frozen at −20°C. Plasma progesterone concentrations were assayed by RIA using a commercial kit (Active Progesterone DSL-3900, Diagnostic Systems Laboratories Inc., Webster, TX). Test sensitivity was 0.12 ng/mL. The intraassay CV was 3.6%. A ewe was considered to be cyclic when the first plasma sample showed a progesterone concentration greater than 1 ng/mL.

Blood also was sampled from 2 subgroups of 15 ewes (group A at cycle 2) exposed to the artificial photoperiod to measure the plasma melatonin concentration. Blood was collected at 2-h intervals for 24 h during one LD period (25 d after the start of LD) and one SHD period (110 d after the start of SHD). Additional samples were taken 30 min before and after the lights turned on and off. Light sticks, providing less than 1 lx at sheep eye level, were used to facilitate blood sampling at night. The samples were collected by jugular venipuncture into 10-mL Vacutainer heparin tubes. They were kept on ice until centrifugation (20 min at 1,800 × *g* at room temperature) within 1 h of collection. The plasma was harvested and frozen at −20°C. Melatonin was assayed in duplicate by RIA using a method described previously by Malpaux et al. (1993). The detection threshold was 4 pg/mL, and the intraassay CV was 6.3%.

Statistical Analysis

For the groups A, B, C, and D treated with photoperiod, only the ewes having been exposed to a complete photoperiod treatment of 4 mo of LD and 4 mo of SHD were included in the statistical analyses for a given reproductive cycle. Nonpregnant ewes treated with hormones and transferred to another photoperiod group were not included in the analyses of the reproductive performance of the group receiving these females.

To compare the reproductive performances between the 3 reproductive cycles within each photoperiod group, ANOVA was performed using the MIXED procedure (SAS Inst. Inc., Cary, NC) for continuous variables: interval between ram introduction and conception, mean BCS during the reproductive cycle, number of lambs born, and birth weight of lambs and litter. The main effect included in the model was reproductive cycle (1, 2, 3). Because the same ewes were followed during the entire experiment, reproductive cycles were considered as repeated measures. The Tukey-Kramer multiple comparisons test then was used to evaluate least squares means difference between reproductive cycles (within groups). The categorical variables were analyzed using the LOGISTIC procedure of SAS. Categorical variables included percentage of ewes detected in estrus, fertility rate, and ewe culling rate. Analyses were performed within group with cycle as main factor in the model and CONTRAST statements to assess difference between cycles.

To test whether the season of breeding could influence the performance of ewes maintained under artificial photoperiod, results were reorganized according to the breeding time: matings in September to January

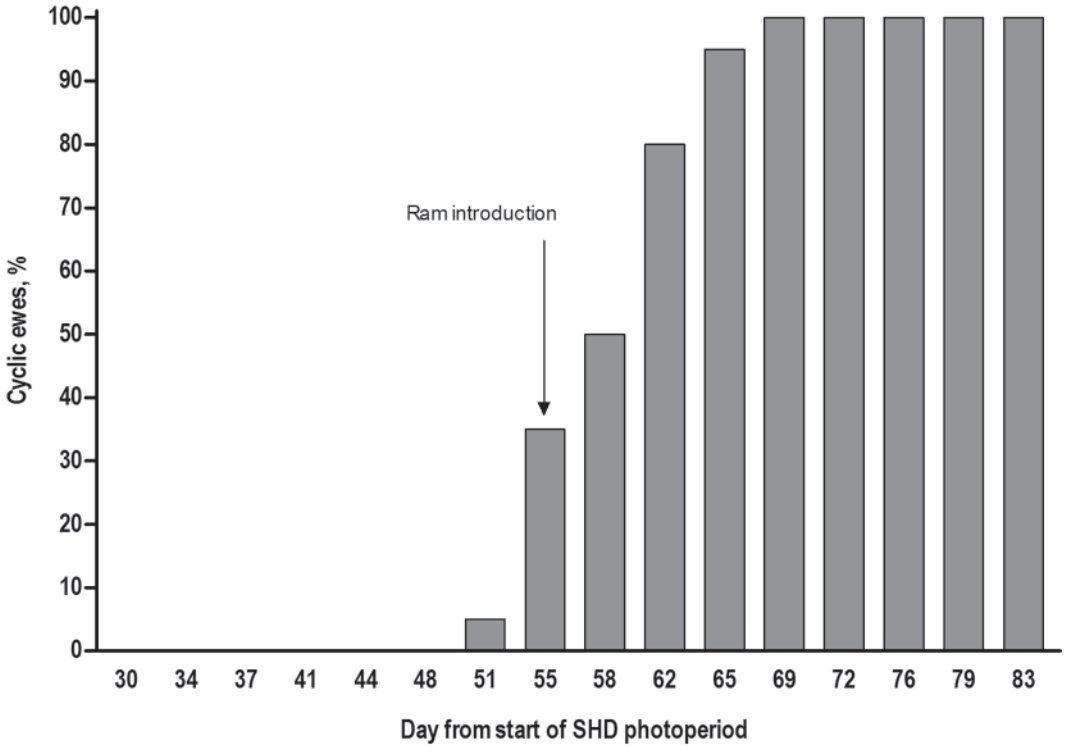

Figure 2. Cumulative frequency (%) of cyclic ewes (n = 20) from the beginning of the short-days sequence (SHD: 8 h of light/d) as indicated by progesterone measurements. Ewe was considered cyclic when one progesterone measurement was >1 ng/mL.

corresponding to natural breeding season and matings in February to August corresponding to out-of-season breeding. Analyses of continuous variables were performed with MIXED procedure using the coding for group × cycle in the model with appropriate CONTRAST and ESTIMATE statements to test the null hypothesis of equality of the 2 mating season means among groups and their interaction. For categorical variables, LOGISTIC procedure was used with group, season, and group × season as main factors.

To compare the results of the photoperiod treatment with those obtained with conventional management (use of intravaginal sponges in out-of-season breeding; control group), the performances of group D under photoperiod treatment were compared with those of the control group. This analysis was possible because the ewes in these 2 treatments were always mated at the same time. For continuous variables, analyses were conducted with the mixed model described previously with proper ESTIMATE statements to assess difference between treatments (photoperiod group D vs. control) among mating seasons (cycles 2 and 3 = out-of-season breeding and cycle 1 = natural breeding season) and their interaction. For categorical variables, main factors included in the model were treatment, season, and treatment × season interaction.

RESULTS

Results presented are exclusively from ewes that were treated with the sequence of photoperiod of 4 mo of LD followed by 4 mo of SHD. Data from nonpregnant ewes after mating in photoperiod and treated with hormones to be rebred in another group are excluded to focus on the direct effect of the photoperiod regimen.

Performance of Ewes Under the Photoperiod Regimen

Based on progesterone concentration profiles, the mean interval between the beginning of SHD and the first estrous cycle was 59.2 d, and all of the ewes ovulated by d 69 (Figure 2). The first ewes displaying estrous behavior did so 51 d after the start of SHD.

The mean interval between ram introduction and conception was 9.4 d for all the photoperiod groups (data not shown). The analysis of the distribution of fertile matings for all the ewes under controlled photoperiod showed that 83.4% of the females were fertilized within the first 18 d of introduction of rams, 6.6% between 19 to 27 d, and 9.9% in the last 8 d of the mating period (Figure 3).

Overall fertility for the 3 breeding periods of the 4 groups under controlled photoperiod was 91.6% (data not shown). No difference in fertility was found between reproductive cycles within groups, except for group A, showing a significant decline in fertility in the second reproductive cycle, during the August-to-September mating period (70.6% for cycle 2 vs. 100% and 91.4% for cycles 1 and 3, respectively; $P < 0.003$; Table 1). Significant interaction group × cycle was observed for prolificacy ($P = 0.002$; data not shown).

The number of culled ewes under photoperiod treatment was 39 for the 2 yr. The culling rate for the ewes

Table 1. Evolution of reproductive performance of the 4 groups of ewes (groups A to D) treated with a photoperiod regimen alternating 4 mo of long days (16 h of light/d) and 4 mo of short days (8 h of light/d) in 3 successive reproductive cycles

	Reproductive cycle				
Trait	1	2	3	SEM	*P*-value
Group A					
Date of ram introduction	Nov. 23	Aug. 1[1]	Apr. 7[1]		
No. of ewes exposed	52	52	36		
Fertility at lambing, %	100.0	70.6	91.4		0.003
Interval first-exposure-to-conception, d	6.0[a]	21.6[b]	5.7[a]	1.3	<0.0001
No. of lambs born/lambing	2.37	2.58	2.78	0.17	0.159
Group B					
Date of ram introduction	July 27[1]	Apr. 3[1]	Nov. 29		
No. of ewes exposed	47	43	35		
Fertility at lambing, %	97.9	90.7	88.6		0.289
Interval first-exposure-to-conception, d	16.2[a]	13.3[a]	5.1[b]	1.7	<0.0001
No. of lambs born/lambing	2.35[a]	3.18[b]	2.63[a]	0.23	0.0004
Group C					
Date of ram introduction	Feb. 6[1]	Oct. 4	June 6[1]		
No. of ewes exposed	54	47	51		
Fertility at lambing, %	98.1	100.0	88.2		0.083
Interval first-exposure-to-conception, d	5.8[a]	7.6[ab]	9.8[b]	0.9	0.007
No. of lambs born/lambing	2.96	2.83	2.70	0.14	0.377
Group D					
Date of ram introduction	Oct. 15	June 6[1]	Feb. 5[1]		
No. of ewes exposed	58	50	43		
Fertility at lambing, %	91.2	88.0	95.0		0.524
Interval first-exposure-to-conception, d	10.3[a]	8.8[ab]	3.8[b]	1.7	0.018
No. of lambs born/lambing	2.78	2.67	2.98	0.17	0.341

[a,b]For continuous variables, within a row, least squares means without a common superscript differ ($P < 0.05$).
[1]Mating periods corresponding to out-of-season breeding.

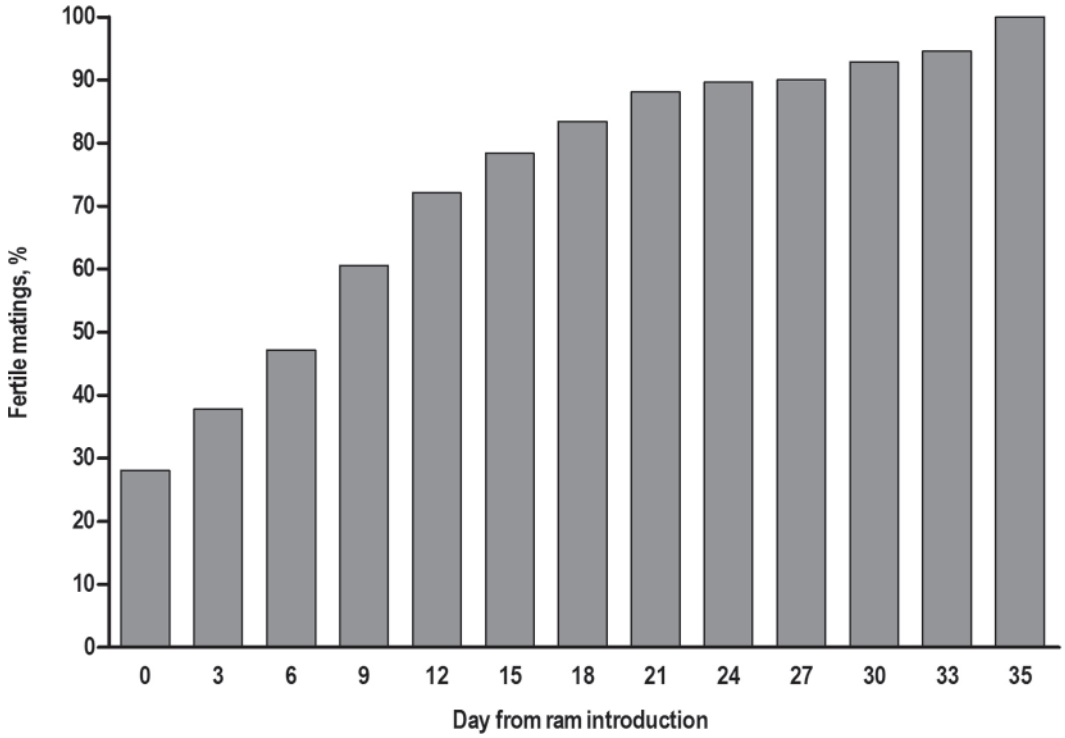

Figure 3. Cumulative frequency (%) of fertile matings for all the breeding periods of the 4 groups of ewes (n = 513) exposed to the alternating 4-mo sequences of short days (8 h of light/d) and long days (16 h of light/d).

Table 2. Effect of the breeding season on the reproductive performance of the 4 groups of ewes[1] (A to D) treated with a photoperiod regimen alternating 4 mo of long days (16 h of light/d) and 4 mo of short days (8 h of light/d)

	Breeding season[2]			*P*-value	
Trait	Season	Out-of-season	SEM	Season	Group × season
Fertility at lambing, %	95.3	89.7		0.085	0.042
Interval first-exposure-to-conception, d	7.1	10.5	0.7	<0.0001	<0.0001
No. of lambs born/lambing	2.65	2.78	0.07	0.160	0.331
Lamb weight at birth, kg	3.6	3.4	0.1	0.002	0.001
Litter weight at birth, kg	8.7	8.4	0.2	0.231	0.004
Mean BCS	2.6	2.7	0.03	0.01	0.002
Ewe culling rate, %	7.3	6.4		0.788	0.902

[1]Respectively, 192 and 376 breeding opportunities for season and out-of-season breeding.
[2]Season: matings in September to January; out-of-season: matings in February to August.

under controlled photoperiod showed the same trend between groups and reproductive cycles (group × cycle; $P = 0.802$; data not shown). The rates were identical between reproductive cycles within a given group ($P = 0.370$).

When considering only ewes that received the 4-mo LD and SHD light sequences, the annual productivity of the photoperiod treatment was 1.38 lambing/ewe and 3.78 lambs/ewe (data not shown).

Effects of Season of Breeding in Photoperiod-Treated Ewes

Analyses performed to explore the effect of the season of breeding on the performance of ewes under photoperiodic control showed an interaction between mating season and group for fertility rate ($P = 0.042$; Table 2). Fertility for the photoperiod treated groups mated during the nonbreeding season tended to be less compared with those mated in the breeding season for group A only (79.1 vs. 100.0%; $P < 0.1$). The same interaction was also revealed to be present for first-exposure-to-conception interval ($P < 0.0001$; Table 2). Groups A and B showed longer delay to conceive in the nonbreeding season than in the natural breeding season (+7.6 and +9.9 d, for groups A and B, respectively; data not shown), whereas group C had comparable intervals regardless of the season and group D had a shorter interval when mated out-of-season (−4.0 d; data not shown).

Ewes mated during the natural nonbreeding season showed similar prolificacy than those bred in the breeding season ($P = 0.16$; Table 2). For the litter weights, no difference was observed between breeding seasons (Table 2).

Comparison Between Photoperiodic and Control Groups

An interaction of season and treatment was observed when comparing fertility of ewes in group D, exposed to photoperiodic treatment, and control group, managed under natural variation in day length ($P = 0.051$; Table 3). For mating in the natural breeding season, analyses showed no difference in fertility between group D and the control group (91.2 vs. 97.2% for group D and the control group, respectively; $P = 0.277$; data not shown). However, in the nonbreeding season, ewes in the photoperiod program reached a significantly greater fertility rate than control group treated with intravaginal sponges and eCG (91.1 vs. 76.3% for group D and control group, respectively; $P = 0.016$; data not shown).

The prolificacy of group D, exposed to photoperiod, was greater than that of the control group during both seasons of mating (2.81 vs. 2.27; $P = 0.0002$; Table 3). No difference was observed in litter birth weight between both groups ($P = 0.543$; Table 3).

Ewes in group D exposed to the photoperiod regimen lambed 1.33 times and produced 3.74 lambs/yr, whereas the control ewes reached annually 1.24 lambing/ewe with 2.79 lambs/ewe (data not shown).

Perception and Light Intensity

Figure 4 illustrates the pattern of melatonin secretion over a 24-h period in ewes exposed to LD or SHD. In LD (Figure 4a), melatonin concentrations were greatest during the hours of darkness and least in the daylight (103.3 vs. 10.8 pg/mL; $P < 0.0001$). In SHD (Figure 4b), the nighttime melatonin concentration was also greatest and the daytime concentration least (104.7 vs. 6.7 pg/mL; $P < 0.0001$).

DISCUSSION

Performance of Ewes Under the Photoperiod Regimen

The sexual activity observed in all groups of ewes under the photoperiodic treatment confirms the effectiveness of the photoperiod regimen to induce estrous behavior regardless of the time of year. Progesterone profiles showed that, at the time of ram introduction, 35% of the ewes were already cycling, whereas 80% of the ewes exhibited luteal activity a week later. These

Table 3. Comparison of the reproductive performance of the ewes[1] in group D treated with a photoperiod regimen alternating 4 mo of long days (16 h of light/d) and 4 mo of short days (8 h of light/d) and control group managed under conventional management

	Treatment (Trt)			*P*-value		
Trait	Photoperiod	Control	SEM	Trt	Season	Trt × season
Fertility at lambing, %	91.2	84.2		0.965	0.048	0.051
Interval first-exposure-to-conception, d	7.6	7.3	1.1	0.106	0.0001	0.251
No. of lambs born/lambing	2.81	2.27	0.11	0.0002	0.409	0.583
Lamb weight at birth, kg	3.4	4.1	0.1	<0.0001	0.291	0.712
Litter weight at birth, kg	8.0	7.7	0.4	0.543	0.489	0.116
Mean BCS	3.0	2.5	0.04	<0.0001	0.412	0.0002
Ewe culling rate, %	8.0	7.3		0.706	0.940	0.368

[1]Respectively, 151 and 97 breeding opportunities for photoperiod treatment and control.

last results, in addition to the short mean interval between ram introduction and conception and the fact that more than 80% of the fertile matings occurred in the first 17 d of the breeding period, indicate that this sexual activity was attributable to photoperiod treatment rather than to the ram effect. Indeed, if estrus was induced by the sudden male exposure, intensive breeding would happen mainly 18 and 25 d after ram introduction (Martin et al., 1986; Rosa and Bryant, 2002).

Data on the timing of estrus and fertile matings corroborated previous observations by Chemineau et al. (1988) indicating that sequences of 3 mo of LD and SHD stimulate estrous activity approximately 50 d after the transition to SHD. Studies involving ovariectomized ewes also demonstrated that the alternation between periods of LD and SHD (or melatonin treatment mimicking SHD) induced sexual activity after about 50 to 80 d of exposure to SHD (Karsch et al., 1986; Malpaux et al., 1988a; Ravault and Thimonier, 1988). Besides the alternation between SHD and LD, the duration of the light sequences (120 d in the present experiment) could have contributed to the initiation of sexual activity via the development of photorefractoriness, as observed in ewe after 100 to 150 d of exposure to the same and constant photoperiodic signal by some authors (Karsch et al., 1986; Malpaux et al., 1988b; Bocquier et al., 1997).

Fertility performances were greater than 88% in 11 of the 12 breeding periods for the ewes maintained under photoperiod with an overall mean near 92%. These results obtained from 8 mating periods in natural out-of-season breeding and 4 in natural sexual season were comparable with the percentage normally seen in the natural breeding season for this breed, as confirmed by fertility rate of the control group at this period of the year (97.2%). The fertility rates recorded and their consistency across the reproductive cycles set the present study apart from earlier experiments involving alternating photoperiodic sequences (Ducker and Bowman, 1972; Vesely, 1978; Vesely and Bowden, 1980; Hackett and Wolynetz, 1982, 1985; Vesely and Swierstra,

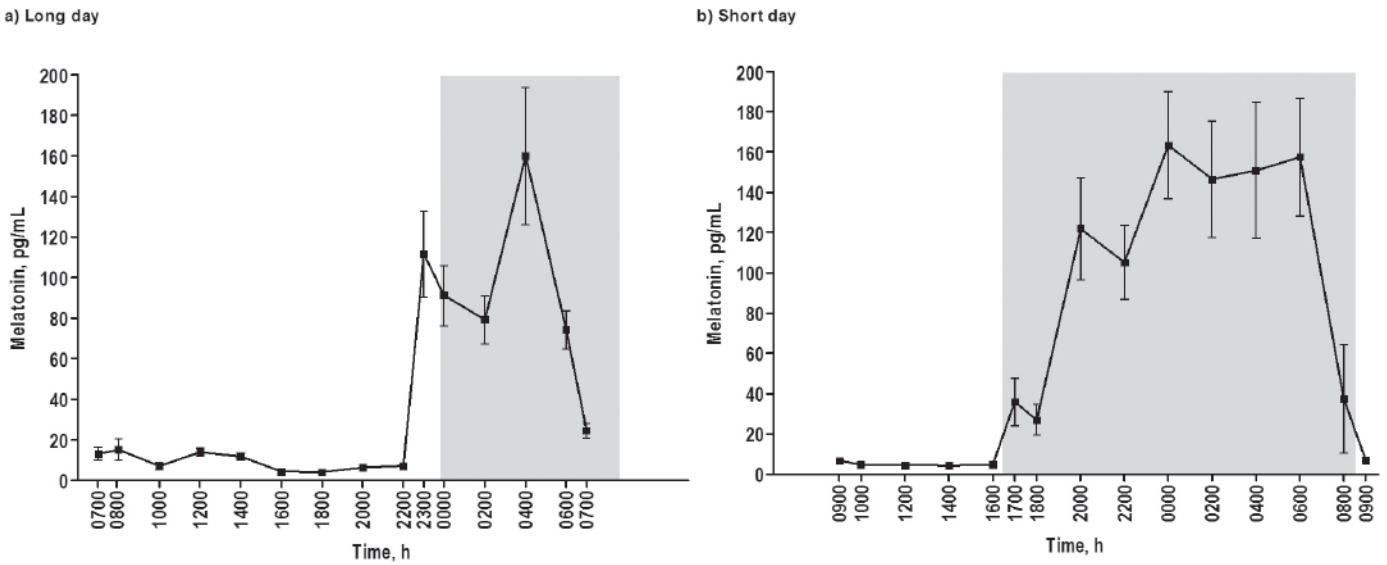

Figure 4. Mean (±SEM) concentrations of melatonin (pg/mL) measured during a 24-h period in a) long day (16 h of light/d) and b) short day (8 h of light/d). Shaded box indicates the darkness period (n = 15 per photoperiod).

1985) that all reported major variations in the fertility rate or declines in fertility after each production cycle. The longer interval between lambing and mating and adequate timing for the ram introduction in the photoperiod sequence could explain the better results in the present study. Moreover, photoperiodic preparation of rams could have contributed to the fertility rates observed as previously demonstrated by Schanbacher (1979) and Fitzgerald and Stellflug (1991). The greater than expected fertility observed for control group treated with vaginal sponges could also be explained by the photoperiodic preparation of the rams. In fact, the fertility rate in hormonal synchronized control ewes, around 76%, is much greater than the rate normally observed for seasonal sheep breeds, such as Arcott Rideau, treated with sponges during this period of the year at similar latitudes (Shrestha et al., 1982; F. W. Castonguay, unpublished data).

Photoperiod-treated ewes in group D had greater litter size than the control group during both seasons, despite the fact that the control ewes received eCG injections during the out-of-season breeding. These results indicate that the photoperiod regimen had a positive effect on prolificacy. A trial led by Dunstan et al. (1977) demonstrated a stimulatory effect of SHD on litter size by exposing ewes to 10 h of light in comparison with females maintained in natural photoperiod. Other studies showed indirect evidence of a stimulatory effect of the SHD on ovulation rate, litter size, or both. Treatment with exogenous melatonin, mimicking SHD, enhanced the ovulation rate or litter size compared with control group bred in nonbreeding season (Poulton et al., 1988; Chemineau et al., 1992; Haresign, 1992). These studies support the difference observed between treatments in the present experiment in out-of-season, because photoperiod groups were in SHD of 8 h, whereas the control group was exposed to natural LD. In sexual season, both groups were submitted to SHD, but the ewes in artificial photoperiod received 8 h of light/d from July to October, whereas the control ewes were exposed to natural decreasing day length between 15.5 to 11 h of light/d. As the duration of melatonin secretion regulates the activity of the hypothalamo-hypophysial and gonadal axis (Karsch et al., 1988), ewes under photoperiod regimen were presumed to secrete more melatonin than control group before and during all the mating periods. Then, we can postulate that the ovarian activity is more strongly promoted in photoperiodically treated ewes compared with the control group under natural variation in day length in both seasons.

Effects of the Season of Breeding in Photoperiod-Treated Ewes

Fertility rates were greater than 88% and comparable in both seasons of breeding for all groups except group A. For this group, only 1 mating in out-of-season (cycle 2) ended by a reduced fertility rate. Because 10 of the 12 nonpregnant ewes in this breeding group presented obvious crayon marks indicating that were mounted by the rams, we suspected the greater temperatures in the barn during this mating period (more than 5 d with temperatures of about 30°C) to have adversely affected fertility or gestation maintenance as previously observed by many authors (Alliston et al., 1961; Dutt, 1964; Shelton and Huston, 1968; Colas, 1980; Chemineau, 1993). These assumptions could also explain the longer first-exposure-to-conception interval during nonbreeding season detected at this mating period.

It is worthwhile to note that the ewes maintained under artificial photoperiod showed similar prolificacy regardless of the time of year in which they were mated. Previous studies on ewes managed under natural photoperiod variations observed that litter size was greater when breeding occurred during the sexual season (Notter and Copenhaver, 1980; Fogarty et al., 1984). The absence of decline in prolificacy for matings in out-of-season in photoperiod-treated ewes confirms the positive influence on the reproductive neuroendocrine axis of the SHD as exploited in our photoperiod program.

Globally, the fact that prolificacy and fertility were as good in season as in out-of-season breeding indicates that the photoperiodic program successfully simulated the natural breeding season.

Perception and Light Intensity

The melatonin secretion profiles observed in ewes in the current study under light control are consistent with existing literature reports. According to Rollag et al. (1978), the melatonin concentration increases rapidly within 2 to 10 min after the start of the dark period and remains at nighttime concentrations (100 to 300 pg/mL) until the lights are turned on. When lights turn on, the melatonin concentrations decline abruptly and return to daytime concentrations, below 30 pg/mL (Notter, 2002), within 5 to 10 min (Rollag et al., 1978).

The melatonin profiles also confirm that the low light intensities of 15 and 35 lx, measured at the sheep eye level, were sufficient to inhibit diurnal secretion of melatonin. This finding is in agreement with the results of Arendt and Ravault (1988), who showed that a light intensity as low as 1.02 lx was sufficient to reduce plasma melatonin concentrations in ewes. Although some technical publications recommend that sheep should be exposed to a light intensity of at least 200 lx to achieve the desired reproductive control (Brice et al., 2003; Pottier and Sagot, 2006), there is no scientific evidence to support this recommendation. Our study indicates that light intensity as low as 35 lx can be used to control the reproductive activity in ewes.

Overall System Productivity

The annual productivity of the photoperiod treatment was 1.38 lambing/ewe and 3.78 lambs/ewe. Globally, when considering ewes exposed to artificial photo-

period plus those treated with intravaginal sponges, the production system resulted annually in 1.39 lambing/ewe and 3.76 lambs/ewe. These productivities were superior to those that can be extrapolated from previous studies on annual photoperiod regimen (Hackett and Wolynetz, 1985; Vesely and Swierstra, 1985). At the end, 69% of the photoperiod-treated ewes lambed 3 times in 2 yr. In the global system (photoperiod plus sponges), 73% did so. The productivity of the current system was also greater than those reported for other types of accelerated lambing systems, like STAR (0.98 lambing/yr; Lewis et al., 1996), Camal and Morlam (1.21 and 1.28 lambing/yr, respectively; Iniguez et al., 1986), or the system of Notter and Copenhaver (1980: 1.27 lambing/yr). The productivity of the photoperiod program tested was achieved with a seasonal breed, contrary to previous systems that are more adapted to nonseasonal breeds by implying natural breeding in out-of-season period.

In conclusion, the present study shows the effectiveness of a photoperiodic program based on continuous alternating 4-mo sequences of LD and SHD in controlling the annual reproductive cycles in ewes. The photoperiodic treatment induced intense estrous activity at any time of the year, leading to greater ewe fertility and prolificacy throughout the year. The performances achieved at every breeding period all over the year were comparable with those normally seen only in the natural breeding season. The effectiveness of this photoperiod program points to the possibility of drastically reducing hormone use in such production systems and even eliminating their use through selection for response to photoperiod treatment.

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Erratum to "Accelerated lambing achieved by a photoperiod regimen consisting of alternating 4-month sequences of long and short days applied year-round" (J. Anim. Sci. 88:3280–3290)

J. Cameron, B. Malpaux, and F. W. Castonguay

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In Figure 4, panel a, the shading was incorrect in the original figure and should begin at 2230 h. The correct figure is shown below. The journal regrets the error.

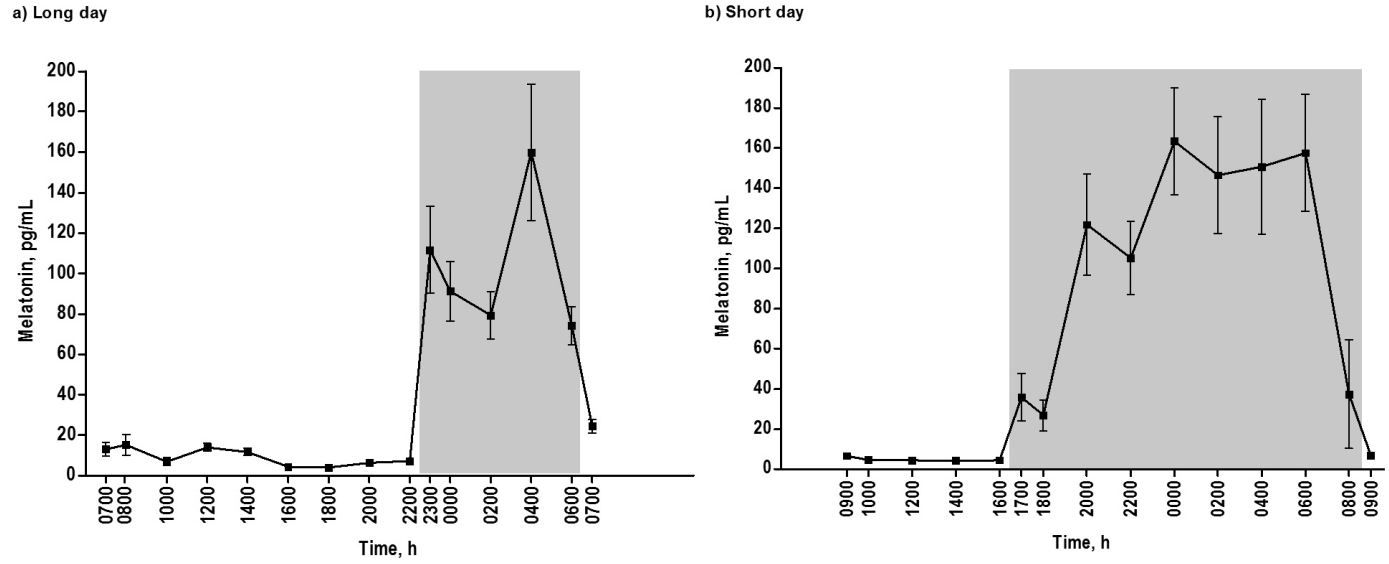

Figure 4. Mean (±SEM) concentrations of melatonin (pg/mL) measured during a 24-h period in a) long day (16 h of light/d) and b) short day (8 h of light/d). Shaded box indicates the darkness period (n = 15 per photoperiod).

Cameron, J., B. Malpaux, and F. W. Castonguay. 2010. Accelerated lambing achieved by a photoperiod regimen consisting of alternating 4-month sequences of long and short days applied year-round. J. Anim. Sci. 88(10):3280–3290.