INTRODUCTION

Previous studies have indicated that seasonal factors influence age at puberty in the bovine female. Heifers born in spring reached puberty at younger ages than those born in autumn or winter (Menge et al., 1960; Roy et al., 1980). Grass et al. (1982) reported a bimodal distribution in age at puberty among autumn-born heifers: some heifers reached puberty in the summer, few reached puberty in the autumn and winter and most became pubertal the following spring. It was not possible to determine the time at which season influenced sexual maturation in these studies, because season of birth was confounded with season of subsequent development.

Separation of these effects is possible when seasonal conditions are altered at predetermined ages. Our objectives were to confirm that season affected age at puberty and to determine the stage of life at which season had its effect. This was accomplished by rearing heifers born in two seasons of the year under natural conditions until 6 months of age, and in environmental chambers designed to simulate temperature and photoperiod characteristic of spring, summer and early autumn (Sp-F chamber) or autumn, winter and early spring (F-Sp chamber).
humidity was kept constant, between 60 and every 7 days to mimic seasonal fluctuations. Relative temperature and photoperiod programs were changed linearly to daily minimum at 2100 h. After 0900 h, temperature increased linearly to 0900 minimum were simulated as follows, A daily

Animals and Treatment

Twenty-eight Angus X Holstein heifers, 14 born on March 21, 1978 (M; vernal equinox) and 14 born on September 23, 1978 (S; autumnal equinox) were purchased at 1 week of age. They were reared until 6 months of age in a three-sided shed open at the south to an exercise paddock so that animals were exposed to natural conditions. Heifers were fed milk replacer until they were able to consume a mixed diet of chopped hay and grain (67% TDN), which they received for the entire experiment. From 6 to 12 months of age, animals were maintained, untethered, in one of two environmental chambers (5.18 x 3.66 m) at the University of Wisconsin Biotron. One chamber was programmed to simulate diurnal fluctuations in dry bulb temperature and photoperiod characteristic of spring, summer and early autumn (March 21-Sept. 23, Sp-F chamber) for Madison, Wisconsin (43° 8' N, 89° 20' W). The other was programmed to simulate conditions of autumn, winter and early spring (Sept. 23-March 21, F-Sp chamber).

Average temperatures and photoperiods during the first year of life are presented in Fig. 1. Two groups, M, F-Sp and S, Sp-F went through naturally occurring temperatures and photoperiods. One group, M, Sp-F, was exposed to the equivalent of two successive spring and summer environments and the other group, S, F-Sp, went through two autumns and winters. In the chambers, dawn and dusk were simulated by using incandescent and fluorescent lighting to produce gradual changes in light intensity (between 0 and 1076 lux in 30 min). Diurnal fluctuations in ambient temperature were simulated as follows. A daily minimum temperature was maintained between 2100 and 0900 h. After 0900 h, temperature increased linearly to reach a maximum at 1500 h. This was followed by a linear decline to the daily minimum at 2100 h. Temperature and photoperiod programs were changed every 7 days to mimic seasonal fluctuations. Relative humidity was kept constant, between 60 and 70%

Throughout the experiment.

While in the chambers heifers were individually fed weighed amounts of the ration. They were allowed access to feed for 2 h in the morning (0900 to 1100 h) and 2 h in the afternoon (1300 to 1500 h) and water was always available at all times. Individual body weights (BW) and feed consumptions were recorded at 28-day intervals. Beginning at 240 days of age, the heifers were checked for estrous behavior by turning a vasectomized bull into each chamber for 15 min each morning (0700 h) and afternoon (1600 h). At other times the bull was kept in a pen between the two chambers, out of view of the heifers. Bulls were changed periodically. Ovarian dimensions and structures were determined by palpation per rectum weekly intervals beginning at 213 (M) or 209 (S) days of age.

Blood samples were collected every 7 days between 6 and 12 months of age to determine serum concentrations of luteinizing hormone (LH), follicle-stimulating hormone (FSH), Prol and T4. Serum concentrations of progesterone were determined in samples collected every 3 days from 246 (M) or 240 (S) days of age until a second corpus luteum was detected. All blood samples were taken at 1200 h via jugular venipuncture. Samples were allowed to clot for 2 h at 20°C and 24 h at 4°C before centrifugation. Serum was recovered and stored at -20°C until analyzed by radioimmunoassay (RIA).

Radioimmunoassays

Serum concentrations of LH were determined using the double antibody RIA developed by Niswender et al. (1969), as validated for use in our laboratory (Schillo et al., 1982a). Concentrations of hormone are expressed in terms of NIH-LH-B10 standard. Initial dilution of first antibody (Niswender B225) was 1:80,000. All serum samples (200-μl aliquots in duplicate) were analyzed in the same assay. The within-assay coefficient of variation (CV) was 7.7% for sera from ovariectomized heifers. The lower limit of detection was 0.4 ng/ml.

Concentrations of FSH were determined by the RIA developed by Bolt (1979) and described by Hansen et al. (1982). All samples were assayed in duplicate using 400-μl sample/tube. Initial dilution of antisemur to the β subunit of FSH was 1:12,500, and concentrations of hormone are expressed as ng USDA-FSH-BP3/ml. Lower limit of detection was 0.51 ng/ml. Within- and between-assay CV's were 7.0% and 4.8%, respectively, for sera from ovariectomized heifers.

The RIA for Prol was performed as described by Forrest et al. (1980) with the following modifications. Prol (USDA-bProl-1-1) was iodinated by reacting 250 μCi Na125I and 2.5 μg chloramine T for 1 min. The reaction was stopped by addition of 10 μg sodium metabisulfite. 125I-Prol was used at a dilution of about 20,000 cpm/100 μl. Initial antibody dilution was 1:240,000 in a 0.1 M PO4 solution, pH 7.5, containing 0.9% NaCl, 1.9% ethylenediamine tetraacetic acid, disodium salt (EDTA) and 1:400 normal rabbit serum; 200 μl of antibody was added to each tube. Assay diluent was 0.1 M PO4 buffer, pH 7.5 with 0.9% NaCl and 0.1% gelatin (PBS-gel). The second antibody used was raised in our laboratory from sheep immunized against rabbit serum and added (200 μl) at an initial
INFLUENCE OF SEASON ON PUBERTY IN HEIFERS

FIG. 1. Temperatures and photoperiods from birth to 12 months of age. Heifers were reared under natural conditions until 6 months of age. At the vernal and autumal equinoxes the heifers were placed in environmental chambers from 6 to 12 months of age and exposed to temperatures and photoperiods characteristic of spring, summer and early autumn (chamber Sp-F) or autumn, winter and early spring (chamber F-Sp). Lines represent average daily photoperiods by week of age and shaded areas the range of daily minimum and maximum temperatures, averaged by week of age.
dilution of 1:30 in PBS-EDTA. The percent binding when no cold hormone was present (B0) averaged 35% and when no first antibody was present averaged 3.6%. Samples were initially assayed at 100 μl/tube in duplicate. Samples in which percent binding was greater than 90% B0 or less than 10% B0 were reassayed at 400 or 50 μl, respectively. Inhibition of binding of 125I-Pro by increasing amount of standard (NIAMDD-Pro-B6, range 0.2 to 50 ng/tube) or volume of sera from pregnant cows was linear (P<0.01) and the responses were parallel. Percent recoveries (amount measured/amount added) were 128 and 108% when 5 or 10 ng Prl was added to pregnant cow sera. The assay sensitivity was 0.16 ng/tube. Within- and between-assay CV’s were 9.5% and 18.0%, respectively, for pregnant cow sera.

Serum concentrations of progesterone were measured by the RIA developed by Staigmiller et al. (1979a). Serum aliquots of 500 μl were extracted with 5 ml glass distilled hexane and reconstituted with 500 μl 0.01 M PBS-gel, pH 7.1 prior to RIA. Procedural losses of [3H]progesterone added to serum averaged 30%. Initial dilution of antibody was 1:10,000. Inhibition of binding of 125I-progesterone by increasing amount of standard (36–11,200 pg/tube) was linear (P<0.01) and parallel to the inhibition achieved by adding increased volume of sera from pregnant cows. Percent recoveries when known quantities of standard ranging from 0.25 to 1.0 ng were added to sera from adrenalectomized, ovariectomized heifers ranged from 97 to 107%. The assay sensitivity averaged 0.36 ng/ml after correction for losses during extraction. Within- and between-assay CV’s were 8.7% and 8.8%, respectively, for sera from pregnant cows.

Concentrations of T4 were determined in sera obtained at monthly intervals using a commercial RIA kit marketed by Amersham (IM 0.92). The system includes anti-T4 serum, polyethylene glycol to precipitate antigen-antibody complexes, [125I]T4 and T4 standards in concentrations of 0.2, 3.7, 10.7 and 20.2 μg/dl human serum. A portion of the 3.7 μg/dl standard was diluted with charcoal-treated serum from ovariectomized cows to yield a 1.85 μg/dl standard. Plots of logit (fraction of bound [125I]T4) versus log (concentration of standard) were linear (P<0.01) for the 1.85 to 20.2 μg/dl range. Inhibition of binding by adding increased volume of sera from pregnant cows was also linear (P<0.02) and parallel to the standard curve. The correlation between amount of standard added to cow serum (10.1, 5.35 and 1.85 μg/dl) and the amount measured by the assay (12.8, 6.2 and 3.8 μg/dl) was high (r=0.98). Within- and between-assay CV’s for pregnant cow sera were 3.7% and 11.0%, respectively.

Statistical Analysis

Age at puberty was defined as the age at which progesterone concentrations exceeded 1 ng/ml for at least three samples, signifying a luteal phase of 9 to 15 days in length. We stopped taking blood samples in three animals (2 M, F-Sp and 1 M, Sp-F) before the first prolonged elevation in progesterone because they became pubertal after leaving the chambers. Age at puberty in these heifers was defined as 10 days prior to the detection of the first corpus luteum by rectal palpation. The effects of date of birth and chamber on age and weight at puberty were evaluated by analysis of variance after log transformation, since heterogeneity of variance (P<0.05) was indicated for both these traits by Bartlett’s test (Steel and Torrie, 1960).

The length, width and thickness of each ovary were determined by palpation at weekly intervals. The product of these measurements was an estimate of ovarian volume. Total volume for each pair of ovaries was calculated for statistical analyses. These data were reported previously by Hansen et al. (1981).

Heifers in the F-Sp groups were heavier than heifers in the Sp-F groups throughout the experiment. Since BW could be correlated with feed consumption, average daily gain (ADG) and feed efficiency, the effect of date of birth and chamber on growth traits was evaluated by analysis of variance with BW at 6 months as a covariate.

Average monthly concentrations of LH, FSH and Prl were calculated for each animal by averaging weekly values. Kruskal-Wallis tests were used to determine effects of months of birth and chamber on monthly concentrations of LH and FSH. When significant, Dunn’s multiple comparison test (Hollander and Wolfe, 1973) was used to determine which groups differed. Concentrations of Prl (after log transformation) and T4 were subjected to analysis of variance for a split plot in time design, using the conservative F test described by Gill and Haf’s (1971).

RESULTS

Age at Puberty

The cumulative frequency distributions of ages at puberty are presented in Fig. 2. Heifers born in September reached puberty at younger ages than those born in March (P<0.06, Table...
1), and exposure to Sp-F conditions hastened onset of puberty in both groups (P<0.08). Serum concentrations of progesterone remained below detectable levels (<0.36 ng/ml) for most of the prepubertal period. Elevations of progesterone above 1 ng/ml for less than three consecutive samples were detected in 2 M, Sp-F, 4 M, F-Sp, 3 S, Sp-F and 3 S, F-Sp heifers. These concentrations were present in one or two serum samples taken at 3-day intervals (Fig. 3) and preceded the first long-term (> three samples) rise in progesterone. In 3 of the 12 heifers showing these short-term elevations in progesterone, luteal structures were detected by rectal palpation near the time of progesterone increase. These luteal structures were palpated once (2 animals, mean diameter=9 mm) or twice (1 animal, mean diameter=25 mm).

Estrus was associated with the pubertal rise in progesterone concentrations (above 1 ng/ml for three consecutive samples) in 1 heifer from each group. Corpora lutea were detected during the long-term progesterone increases in all of the September-born heifers and in 9 of the heifers born in March. Progesterone concentrations were elevated above 1 ng/ml for five samples for heifers in which no corpora lutea were detected, indicating a luteal phase of normal length (>15 days).

**Growth, Feed Consumption and Feed Efficiency**

We measured these growth related traits for two reasons: 1) to determine if season affected onset of puberty by affecting growth rate since prepubertal weight was found to be related to onset of puberty (Menge et al., 1960; Quirke, 1978; Grass et al., 1982) and 2) to determine if

**TABLE 1. Effects of month of birth and chamber on age and body weight at puberty.**

<table>
<thead>
<tr>
<th>Date of birth</th>
<th>Chamber (after 6 months)</th>
<th>Age at puberty&lt;sup&gt;a&lt;/sup&gt; (days)</th>
<th>Weight at puberty&lt;sup&gt;b&lt;/sup&gt; (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>March 21</td>
<td>Sp-F</td>
<td>321</td>
<td>281</td>
</tr>
<tr>
<td>March 21</td>
<td>F-Sp</td>
<td>346</td>
<td>318</td>
</tr>
<tr>
<td>September 23</td>
<td>Sp-F</td>
<td>295</td>
<td>268</td>
</tr>
<tr>
<td>September 23</td>
<td>F-Sp</td>
<td>319</td>
<td>306</td>
</tr>
<tr>
<td>Date of birth means</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>March 21</td>
<td></td>
<td>334</td>
<td>300</td>
</tr>
<tr>
<td>September 23</td>
<td></td>
<td>307</td>
<td>287</td>
</tr>
<tr>
<td>Chamber means</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp-F</td>
<td></td>
<td>308</td>
<td>274</td>
</tr>
<tr>
<td>F-Sp</td>
<td></td>
<td>333</td>
<td>312</td>
</tr>
</tbody>
</table>

<sup>a</sup>There were effects of date of birth (P<0.06) and chamber (P<0.08).

<sup>b</sup>There was an effect of chamber (P<0.01).
puberty occurred at a common body weight, as reported to occur in rats (Kennedy and Mitra, 1963) and humans (Frisch and Revelle, 1970).

BW of heifers between 6 and 12 months of age are shown in Fig. 4. Season of the first 6 months of life did not influence BW, but heifers in the F-Sp groups were slightly heavier (P<0.10) than Sp-F heifers at all ages except 46 weeks.

Between 6 and 9 months of age, S had greater (P<0.01) mean ADG and feed consumption than M while ADG was greater (P<0.05) for F-Sp than for Sp-F (Table 2). Feed efficiency between 6 and 9 months of age was not affected by date of birth or chamber. Significant differences in ADG, feed consumption and feed efficiency between 9 and 12 months of age were attributed to responses of the M, Sp-F animals. Greater gains between 9 and 12 months of age in this group may have resulted from compensatory gain, since this group gained the least between 6 and 9 months of age.

BW at 7 months of age was negatively correlated with age at puberty in three of four groups (Table 3). Although age at puberty was related to prepubertal weight, heifers did not attain puberty at a common BW (Table 1). Generally, age at puberty was positively correlated with BW at puberty within a group (r=0.09, 0.69, 0.62 and 0.78 for S, Sp-F and F-Sp and M, Sp-F and F-Sp, respectively).

**Serum Concentrations of T4 and Prl**

Neither date of birth nor chamber significantly influenced serum concentrations of T4 (Fig. 5). There was a date of birth X chamber interaction (P<0.023). This interaction occurred because March-born heifers had higher concentrations of T4 at the time they entered the chambers than September-born heifers. The M, F-Sp heifers maintained high T4 levels, while in the September-born group, F-Sp conditions increased T4 levels. The September-born heifers exposed to Sp-F maintained their initial low levels while serum T4 concentrations decreased in the March-born heifers exposed to the Sp-F environment.

Concentrations of Prl in prepubertal heifers paralleled changes in temperature and photoperiod (Fig. 5), being high during long photoperiods and warm temperatures. A significant chamber X time interaction (P<0.005) resulted as Prl concentrations increased with time in Sp-F heifers exposed to increasing day length and temperature, and decreased in F-Sp heifers exposed to decreasing day length and temperature. The significant (P<0.005) date of birth X time interaction was due to different patterns of Prl displayed in Sp-F heifers born in March and September. Concentrations of Prl in Sp-F heifers born in September increased to maximum levels at 30–33 weeks of age, and then remained constant. In contrast, Prl concentrations in March-born heifers exposed to the same conditions reached maximum levels at 38–41 weeks of age and then decreased.

**Serum Concentrations of Gonadotropins**

Serum concentrations of LH were not normally distributed because many values were below the limit of detection of the assay. This skewed distribution was probably the result of infrequent LH pulses during much of the prepubertal period (Schillo, 1981). Nonparametric statistical procedures were used to make comparisons between age groups because the nonnormal distribution of data precluded the use of analysis of variance.

The most striking differences resulted from
## TABLE 2. Effect of date of birth and chamber on average daily gain (ADG), feed consumption and feed efficiency.a

<table>
<thead>
<tr>
<th>Date of birth</th>
<th>Chamber (after 6 months)</th>
<th>ADG (kg/day)</th>
<th>Feed consumption (kg)</th>
<th>Feed efficiency (kg feed)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>6–9 months 9–12 months</td>
<td>6–9 months 9–12 months</td>
<td>6–9 months 9–12 months</td>
</tr>
<tr>
<td>March 21</td>
<td>Sp-P</td>
<td>0.86 0.925*</td>
<td>567 795**</td>
<td>7.92 10.45†</td>
</tr>
<tr>
<td>March 21</td>
<td>F-Sp</td>
<td>0.96 0.77</td>
<td>627 868</td>
<td>7.77 13.68</td>
</tr>
<tr>
<td>September 23</td>
<td>Sp-P</td>
<td>1.00 0.86</td>
<td>659 870</td>
<td>7.90 12.29</td>
</tr>
<tr>
<td>September 23</td>
<td>F-Sp</td>
<td>1.06 0.86</td>
<td>666 864</td>
<td>7.34 12.02</td>
</tr>
<tr>
<td><strong>Date of birth means</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>March 21</td>
<td></td>
<td>0.91††</td>
<td>590†† 831**</td>
<td>7.84† 12.06††</td>
</tr>
<tr>
<td>September 23</td>
<td></td>
<td>1.03b</td>
<td>662b 867b</td>
<td>7.71† 12.19b</td>
</tr>
<tr>
<td><strong>Chamber means</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sp-P</td>
<td></td>
<td>0.93**</td>
<td>613a 833b</td>
<td>7.91a 11.37a**</td>
</tr>
<tr>
<td>F-Sp</td>
<td></td>
<td>1.01b 0.82a</td>
<td>646a 866b</td>
<td>7.65a 12.85b</td>
</tr>
<tr>
<td>MSE</td>
<td></td>
<td>0.090 0.110</td>
<td>50.9 43.9</td>
<td>0.970 1.70</td>
</tr>
</tbody>
</table>

a,b Means with different superscript letters differ at significance level indicated.

c Date of birth × chamber interaction at significance level indicated.

*P<0.10,
**P<0.05,
†P<0.025,
††P<0.01.
the high incidence of nondetectable LH levels in March-born heifers. Eleven of 14 animals in this group had very low concentrations of LH during the first 4 to 6 weeks in the chamber (Fig. 6). In contrast, concentrations of LH during this period were high and variable in 12 of 14 September-born animals (Fig. 6).

These data are summarized in Fig. 7. Mean concentrations of LH in September-born heifers were greater than those in March-born heifers from 26 to 29 weeks of age. The September-born animals also had larger ovaries at this time (see Hansen et al., 1981 for details). There were no consistent effects of chamber on LH concentrations, but ovaries of Sp-F heifers tended to be larger than those of F-Sp heifers from 7–12 months of age (Hansen et al., 1981). Generally, heifers with greater concentrations of LH from 26–29 weeks of age and greater ovarian volume at 7 months of age reached puberty earlier (Table 3).

Only about 30% of the serum samples contained detectable amounts (>0.51 ng/ml) of FSH. Therefore, the distribution of concentrations was skewed and data were analyzed by nonparametric procedures. Neither month of birth nor chamber significantly influenced concentrations of FSH (Fig. 7) but they tended to be highest for M, F-Sp heifers, which were oldest at puberty. Concentrations of FSH appeared to decrease with age in all groups. For all groups, heifers with higher FSH from 26–29 weeks of age tended to be older at puberty (Table 3).

**DISCUSSION**

Seasonal conditions extant during both the first and second 6 months of life influenced age at puberty in heifers. Environmental influences

![FIG. 5. Mean temperatures and photoperiods (panel A) and related serum levels of thyroxine (panel B) and prolactin (panel C) from 26–46 weeks of age. Thyroxine concentrations were influenced by date of birth X time (P<0.025). Prolactin concentrations were influenced (P<0.005) by date of birth, chamber, date of birth X time and chamber X time.](image)

**TABLE 3. Correlation coefficients between age at puberty and various traits measured before puberty.**

<table>
<thead>
<tr>
<th>Trait</th>
<th>March 21</th>
<th></th>
<th>September 23</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sp-F</td>
<td>F-Sp</td>
<td>Sp-F</td>
</tr>
<tr>
<td>Ovarian volume (7 months)</td>
<td>-.75a</td>
<td>-.49</td>
<td>.50</td>
</tr>
<tr>
<td>BW (7 months)</td>
<td>.04</td>
<td>-.30</td>
<td>-.64</td>
</tr>
<tr>
<td>Mean LH (6–7 months)</td>
<td>.79b</td>
<td>-.47</td>
<td>-.59</td>
</tr>
<tr>
<td>Mean FSH (6–7 months)</td>
<td>.14</td>
<td>.27</td>
<td>.29</td>
</tr>
</tbody>
</table>

aP<0.10.
bP<0.05.
during the first 6 months of life may have influenced onset of puberty by altering growth rate, since body weight prior to puberty was related to age at puberty in this and other studies (Menge et al., 1960; Quirke, 1978; Grass et al., 1982) and September-born heifers grew at a faster rate from 6 to 9 months of age. The younger ages at puberty in September-born animals may also have resulted from accelerated ovarian growth brought about by the greater LH release in this group prior to 30 weeks of age. Because we did not regulate environment during the first 6 months of life, but only controlled birth date, further research is needed to determine the specific components of environment during this stage of life that affected the rate at which animals became pubertal.

Exposure to conditions of Sp-F between 6 and 12 months of age hastened onset of puberty in heifers regardless of time of birth. This was probably due to the effects of light, temperature or their combination. Preliminary observations from Peters and Tucker (1978) indicated that long photoperiod hastened puberty in heifers.

Treatment after 6 months of age did not appear to influence age at puberty by altering growth rate, since the earlier age at puberty for Sp-F heifers was not associated with more rapid increases in BW. The lack of association between increased day length and increased ADG in heifers is in disagreement with the results of Peters et al. (1978), who reported that supplemental lighting during the winter increased ADG. Roche and Boland (1980) found that photoperiod did not affect growth rate in bull calves or steers. Our experiment differs from that of Peters et al. (1978) in that temperature followed patterns similar to those of photoperiods and differences in temperature might have masked the effects of photoperiod on growth. In any case, it is unlikely that chamber influenced age at puberty by altering growth.
Generally, treatment after 6 months of age did not significantly influence concentrations of LH. However, we did not evaluate responsiveness of the hypothalamic-pituitary axis to ovarian steroids. Since prepubertal heifers exhibit changes with age in response to the positive (Staigmiller et al., 1979b; Schillo, 1981) and negative (Schillo et al., 1982a) feedback actions of estradiol, it is possible that chamber influenced age at puberty by affecting the maturation of these feedback systems. Hansen et al. (1982) observed that ovariectomized heifers exposed to 18 h light/day released more LH after estradiol injection than heifers exposed to natural winter photoperiods.

FSH concentrations seemed to decrease with age in all groups. Gonzalez-Padilla et al. (1975) reported a small, short-term decrease in both concentrations and variability in concentrations of FSH between 38 and 20 days preceding first estrus in heifers. Serum levels of FSH also decreased with age in prepubertal rats (Dohler and Wuttke, 1975; Ramaley, 1979). The age-related decline in FSH levels in our experiment may have resulted from increased production of inhibin produced by growing follicles (Schwartz and Channing, 1977), as ovarian volume and numbers of large follicles increased as animals became older (Hansen et al., 1981). The group oldest at puberty (M, F-Sp) had the highest concentrations of FSH, possibly because ovarian development was least in this group.

Thyroid activity could affect the onset of puberty by acting directly on reproductive organs (Greeley and Mahesh, 1978) or by altering metabolic or growth rates. In other studies, thyroid activity (Lundgren and Johnson, 1964; Youssef et al., 1967) and serum T4 concentrations (Hurley et al., 1980) were negatively related to ambient temperature, but did not appear to be influenced by day length (Leining et al., 1980). In view of these studies, our results were somewhat surprising. At the beginning of the sampling period in late September, the March-born heifers had higher serum levels of T4 than the September-born heifers, first bled in late March, even though temperatures during these times were higher for March-born heifers. As expected, warm temperatures in the chambers were associated with low levels of T4 and cold temperatures were associated with high levels, although the differences were not statistically significant.

Koprowski and Tucker (1973) have shown that concentrations of Prl in cattle are high during summer and low during winter. This difference was attributed to changes in ambient temperature (Wetteman and Tucker, 1974; Tucker and Wettemann, 1976) and day length (Bourne and Tucker, 1975; Peters and Tucker, 1978). In our studies, Prl concentrations were low when temperatures were cool and day lengths short. Changes in Prl secretion may have been responsible for the chamber effect on age at puberty, but to our knowledge no one has reported an association between serum Prl levels and sexual development of heifers. In general, concentrations of Prl appeared to be influenced by environmental conditions rather than age. Schams and Reinhardt (1974) showed that seasonal patterns of Prl for the first year of life were similar to patterns for the second year of life.

Frisch and Revelle (1970) have reported a "critical" BW necessary for the attainment of puberty. The positive, within-group correlation between age and BW at puberty indicates that heifers treated alike did not reach puberty at a common BW, but rather that animals which were older at puberty were also heavier. Because BW's at puberty differed between groups in our study, it seems that neither date of birth nor chamber affected age at puberty by altering the time at which a "critical" BW occurred.

Very few pubertal ovulations (as indicated by elevations in progesterone for at least three samples) were accompanied by behavioral estrus, presumably because of the unusual conditions for these animals that prevailed in the chambers. Prepubertal rises in progesterone were noted, as they have been in other studies with heifers (Gonzalez-Padilla et al., 1975; Shotton et al., 1978). This prepubertal increase has been shown to come from luteal tissue located beneath the surface of the ovary (Berardinelli et al., 1979).
above 17°C throughout this year. The experiment reported by Menge et al. (1960) also involved Holstein cattle raised under dairy conditions. Therefore, it is unlikely that these animals were exposed to natural temperatures and photoperiods. Unlike the experiments of Menge et al. (1960) and Roy et al. (1980), in which dates of birth may have varied considerably within season, the birth dates of the heifers in our experiments were within a day of the vernal and autumnal equinoxes and heifers were therefore exposed to the same environment at the same ages. In the experiments of Menge et al. (1960) and Roy et al. (1980), season of birth was confounded with seasons at all other ages. For example, the average age at puberty in the study of Menge et al. (1960) was 328 days of age for spring-born heifers and 390 days of age for winter-born heifers. Thus, heifers born in spring became pubertal in the spring and winter-born heifers became pubertal in the winter.

The younger age at puberty of the S, Sp-F group suggests a mechanism by which cattle would tend to calve in the spring and summer regardless of birth date. Autumn-born heifers would reach puberty at less than a year of age, in the summer or early autumn after their birth. Spring-born heifers, older at puberty, would tend to reach puberty and calve in the spring or summer. Long postpartum anestrus periods for cows calving in the winter (Buch et al., 1955; Hansen and Hauser, 1983) also would tend to move calving dates toward spring or summer.

Though we are not sure which environmental conditions prior to 6 months of age affected subsequent onset of puberty, the possibility exists that conditions hastening puberty early in life may have delayed it later. Exposure to short photoperiods and temperatures prior to 6 months of age was associated with early age at puberty while exposure to the same conditions after 6 months of age delayed onset of puberty. Therefore, response of reproductive function to a given environment may change with age.

In conclusion, seasonal factors during the first and second 6 months of life affected onset of puberty in heifers. Even though cattle are not seasonally anestrous as are sheep or hamsters, certain aspects of their reproduction are influenced by season, perhaps in such a way as to concentrate calving dates in certain times of the year. The effect of season on age at puberty may be mediated by changes in growth rate, ovarian size, or secretion of LH or PRL. Subsequent research is necessary to determine how season exerts its effect.ACKNOWLEDGMENTS

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