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ABSTRACT: Effects of environmental factors such as ewe age, season of exposure, and time from lambing to exposure on fertility were evaluated using records on 1,084 Dorset ewes in the STAR accelerated lambing system. The STAR program consisted of five 30-d concurrent breeding and lambing periods per year beginning on January 1, March 15, May 27, August 8, and October 20. Fertility in the flock changed in a cyclic and predictable fashion during the year. Changes in prolificacy were less consistent but also tended to show cyclic variation. Matings that occurred within the typical breeding season (August, October, and January) were more fertile than those occurring in March and June. However, fertility also varied with the age of the ewe and the time since the ewe's last lambing. Except in June, fertility at the first postpartum mating increased as ewes aged. In March and June matings, adult ewes that had just weaned lambs were less fertile than ewes that had failed to conceive in the previous season and therefore had longer postpartum intervals. However, in October and January, ewes that had just weaned lambs were more fertile. A matrix of expected pregnancy rates, or probabilities of fertility, was constructed using a mixed GLM to describe the combined effect of season, ewe age, and time since lambing on ewe fertility in accelerated lambing.

Key Words: Accelerated Lambing, Fertility, Sheep, Dorset, Prolificacy

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Introduction

One way to increase the numbers of lambs born within a flock is to increase the frequency of lambing, which, in turn, requires that a proportion of the ewes exhibit estrus in spring. Estrous behavior can be induced in spring by light and hormone treatment, but this approach requires confinement of animals and considerable inputs of labor, housing, and energy. An alternative is to extend the fertile period by altering gene frequencies to cause permanent and cumulative changes in breeding patterns. The expression of fertility in frequent (or accelerated) lambing systems reflects an interaction of genetic and environmental factors that complicates evaluation of genetic differences among ewes in fertility. With several breeding seasons in a year, some ewes will be pregnant at some mating periods and therefore have no fertility record for such seasons. Ewes that remain nonpregnant, on the other hand, contribute a fertility record at each mating season and will continue doing so until they become pregnant. As a consequence, the average genetic merit of ewes exposed in different seasons may differ because of selection for fertility at previous seasons.

The STAR accelerated lambing system (Hogue, 1986) is an intensive lambing system with five lambing seasons per year. Ewes can lamb up to five times in each 3 yr period. The first objective of this study was to summarize the performance of Dorset ewes managed under the STAR system. The second objective was to focus on fertility in ewes and to estimate the effects of four environmental factors and their interactions on its expression. The environmental factors considered were the season of mating, age, time interval between mating and the previous lambing, and number of lambs nursed at the previous lambing.

Materials and Methods

STAR Design

The STAR accelerated lambing system was developed at Cornell University and implemented in the

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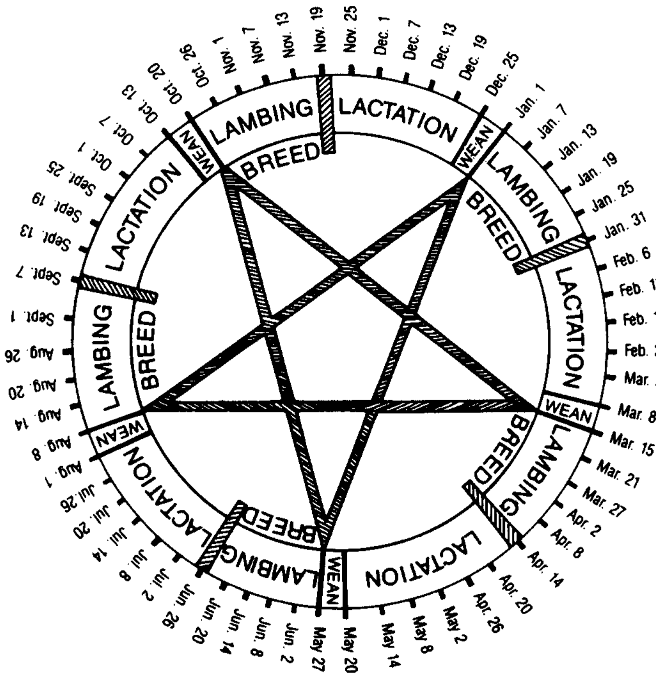

Figure 1. The STAR accelerated lambing system, with five annual, concurrent breeding and lambing seasons beginning on January 1, March 15, May 27, August 8, and October 20. Copyright 1984, Cornell Research Foundation.

Cornell Dorset flock in 1981. In the system, the year was divided into five 73-d seasons that began on January 1, March 15, May 27, August 8, and October 20. The season that began on May 27 will henceforth be referred to as June. A diagram of the STAR system is shown in Figure 1. The beginning of each season corresponds to one of the points of the star. Within each season, breeding of open ewes is concurrent with lambing of ewes that conceived two seasons earlier. Each season ends with weaning of lambs born during the first 30 d of that season.

At the beginning of each season, three distinct groups of ewes were present in the flock: open ewes, ewes that conceived in the preceding season and were in early gestation, and ewes that became pregnant two seasons before and were in late gestation. A proportion of the open ewes had just weaned lambs, whereas others were open because of failure to conceive at earlier opportunities. Ewes in late gestation were identified by visual assessment and palpation of the developing mammary glands and separated from the rest of the flock. Early gestation ewes were not identified and remained with the nonpregnant ewes. All were placed with breeding rams for 30 d at the start of the season. Ewes in late gestation lambed during the same 30-d period. Following lambing, ewes lactated for 36 to 66 d, and lambs were weaned on d 66 of the season. Seven days after weaning, ewes were again placed with breeding rams to begin the next season. The system continued in this manner across seasons with all ewes except those identified as in late gestation exposed to rams in each season.

Breedings in January, August, and October fell within the normal breeding season of sheep and will be referred to as favorable seasons. March and June exposures fell outside the normal breeding season and will be referred to as unfavorable seasons (Dufour, 1974; Fogarty et al., 1984). In the STAR system, the shortest possible mean interval between lambings was 219 d (7.2 mo). Failing this, ewes could lamb after 292 d (9.6 mo) or on an annual (or longer) lambing cycle. Ewes could lamb up to five times in 3 yr (1.67 lambings/yr), which required conception in each of the five seasons. Ewe lambs were exposed to rams at 6 to 7 mo of age and could lamb first at 1 yr of age.

Flock Husbandry

In each season, ewes were exposed to Dorset rams in three single-sire breeding groups. In addition, ewe lambs were routinely exposed to Finnsheep rams and multiparous ewes with long lambing intervals were occasionally exposed to Suffolk rams. Ram to ewe ratios varied widely across breeding groups, years, and seasons, ranging from 5 to 198 ewes per ram, and averaged 50.3 ewes with a SD of 39.7 ewes. Culling of ewes was minimal.

Nonlactating and gestating ewes were maintained on native mixed grass-clover pasture from late April to early September and on hay afterward until mid-January. During winter, ewes received about 1.8 kg dry matter of hay crop silage daily. Ewes were confined for about 70 d during late gestation and lactation and fed approximately 2.3 kg dry matter of hay crop silage daily plus .6 to 1.0 kg/d of grain, depending on the number of lambs being nursed. Lambs were creep fed until weaning at an average age of 55 d.

Experimental Animals and Measures

Lambing records on 1,084 Dorset ewes mated from August 1981 through March 1987 were used. Ewes were daughters of 57 rams; 742 ewes were born in the STAR system and 342 ewes were born in the Cornell alternate month accelerated lambing (CAMAL) system. In the CAMAL system, breeding and lambing occurred in alternate months (Hogue et al., 1980; Iniguez et al., 1986). Rams were selected from twin and triplet litters and(or) from ewes with a history of fall or accelerated lambing. Only one ram born outside the flock was used after the 1983 matings. All rams selected after 1984 had dams with at least five consecutive 7.2-mo lambing intervals. Thirty-six rams were used as service sires within the STAR system.

Records on 7,269 exposures of nonpregnant ewes that resulted in 3,048 lambings and production of 4,642 lambs were available (Table 1). Measurements

Table 1. Numbers of ewes, matings, lambings, and lambs born by mating season

Mating season	No. of ewes mated[a]	No. of exposures	No. of lambings	No. of lambs born
January	557	785	388	553
March	687	1,210	344	477
June	833	1,529	229	349
August	985	2,123	975	1,511
October	939	1,621	1,112	1,752
Total	1,084	7,269	3,048	4,642

[a]Numbers in this column are the numbers of ewes with one or more exposures in the indicated season. The total is the total number of individuals represented across all seasons.

included fertility (1 for ewes that lambed and 0 for ewes that failed to lamb from a given exposure), prolificacy (the size of the litter for ewes that lambed), lambing date, and the lamb's sex, rearing type, and weight and age at weaning. Some of the lambs born in large litters were either fostered or raised artificially if the ewe was judged not to have enough milk to rear them naturally. Only lambs that nursed their dams to weaning were considered reared.

For analysis of fertility, four environmental factors were defined for each exposure. *Mating season* was the STAR season in which the ewe was exposed. *Lambing number* was the number of times the ewe had lambed + 1 and was categorized as one, two, three, or greater than three. *Nursing status* was the number of lambs a ewe nursed to weaning at her most recent lambing (none, one, or greater than one). This categorization was possible only for lambing number two or higher. *Lambing interval* defined the time, in STAR seasons, between a ewe's most recent lambing and her current exposure. At the first exposure following a lambing, the ewe was assigned a lambing interval of one; at each additional exposure prior to conception, the interval was incremented. For ewe lambs, lambing interval was set to one for their first exposure and incremented in the same way following each failure to conceive. Each exposure represented an additional observation.

Inbreeding coefficients were calculated by procedures proposed by Quaas (1976) under the assumption that CAMAL and purchased animals were unrelated. Mean inbreeding coefficients for STAR and CAMAL ewes were 2.6% and .9%, respectively. Lower inbreeding levels for CAMAL ewes partly reflected missing ancestry information in the oldest of the CAMAL ewes. Thus, inbreeding was underestimated (Iniguez et al., 1986). Mean inbreeding increased over time from 1% in 1981 to 2.5% in 1987.

Statistical Analyses

Periodicities. Average fertility changed in a consistent manner across seasons and was described using nonlinear procedures. Average fertility was calculated for each year-season combination, and the linear regression of mean fertility on consecutively numbered year-season combinations (t) was fitted to account for phenotypic trends in fertility. Residuals from this analysis (Y_t) for the t^{th} year-season combination were then described by a periodic model similar to that used by Stroup et al. (1987):

$$Y_t = \alpha_1 \sin(2\pi t/A) + \alpha_2 \cos(2\pi t/A), \qquad [1]$$

where α_1 and α_2 were regression coefficients and A was the interval in seasons between peak performances. Iterative solutions for α_1, α_2, and A were obtained using modified Gauss-Newton methods in the non-linear regression procedure of SAS (1985). Reduced models including only the sine or cosine function were fit to test significance of α_1 and α_2, and A was also fixed at five seasons in both reduced and full models to force a yearly periodicity.

To evaluate possible effects of more stringent culling on fertility, ewes that did not conceive for six consecutive exposures were defined as barren, records following the sixth failure were deleted, and data were reanalyzed. Daughters of these ewes were also removed from the data if they were born at a lambing following truncation of the dam's records.

An annual rhythm of high and low prolificacy similar to that observed for fertility was expected. After removal of time trends by linear regression, the periodic models used for fertility were also fitted for prolificacy.

Fertility. Because ewe fertility took two values (Y = 0 or Y = 1), we defined the probability of fertility as follows:

$$P(Y_i = 0) = 1 - \theta_i \text{ and } P(Y_i = 1) = \theta_i,$$

where θ was the proportion of fertile matings for the i^{th} grouping of explanatory variables. These groupings were based on all combinations of four fixed effects (the ewe's mating season, lambing number, lambing interval, and nursing status) and two random effects (the ewe's sire and dam). Because of small numbers of observations, lambing interval classes of three or more were combined into a single category for these analyses. Sire and dam effects were included to partially account for random genetic effects in estimation of differences among fixed effects. Genetic effects on performance in the STAR system will be considered in greater detail in a later study. Our observations were the number of fertile matings, y_i, given the total number of matings, n_i, that occurred within each grouping of explanatory variables (McCullagh and Nelder, 1989).

We specified a mixed GLM as:

$$\mathbf{y} = \mu + \xi,$$

where $\mathbf{y}$ was the vector of observations, and ξ was the vector of residual errors. The explanatory variables were related to the vector of means ($\boldsymbol{\mu}$) through a monotonic link function $g(\mu)$ such that:

$$g(\mu) = \eta = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{\lambda}$$

(Schall, 1991), where η is a linear predictor combining the vector $\boldsymbol{\beta}$ of our four fixed effects with design matrix $\mathbf{X}$, and the vector $\boldsymbol{\lambda}$ of our two random effects with design matrix $\mathbf{Z}$. Underlying random effects of sires and dams were assumed to have mean 0 and variances σ_s^2 and σ_d^2, respectively. Relationships among sires and dams were not considered in estimation of $\boldsymbol{\beta}$. Because data were binary, we assumed a binomial error distribution. We chose a logit link function, so the transformation between the mean of our data and the linear predictor took the following form (Schall, 1991):

$$g(\mu_i) = \left[\frac{\theta_i}{1 - \theta_i}\right].$$

The model was fit by the method of Schall (1991) using the procedure GLMM (Genstat 5 Committee, 1993). This procedure uses REML (Patterson and Thompson, 1971) to estimate fixed effects and variance components for random effects. Means were estimated on the logit scale and then back-transformed to the original (probability) scale. An approximate 95% CI was determined by doubling the SE on the logit scale for each estimate, subtracting and adding this value to each logit mean, and back-transforming these two bounds to the original (probability) scale. Given the shape of the logit function, these CI are asymmetric.

Nursing status could only be recorded for ewes that had lambed. We therefore initially considered fertility records only for lambing numbers two and higher and included nursing status as a fixed factor. We then considered all fertility records but ignored effects of nursing status. In preliminary analyses, dam effects explained little variation in daughter fertility and this random term was dropped in order to simplify the model.

The initial model was fully saturated in terms of fixed effects; all interactions among fixed effects were included. In a stepwise fashion, progressively simpler models were considered using the Wald statistic as a guide for model selection (Genstat 5 Committee, 1993). The Wald statistic is the ratio of the treatment sum of squares for each fixed level to the residual variance and has a distribution that approximates a chi-square. It is calculated by sequentially removing each fixed term from the model to allow testing of the reduction in sum of squares attributable to that effect after fitting all others. Because the numerical properties of the Wald statistic are not well understood with non-normal distributions (S. J. Welham, personal communication), data were also analyzed fitting only fixed effects in a logit regression procedure (Genstat 5 Committee, 1993) to confirm the results of the mixed-model analyses. A logit link function with a binomial error distribution was again used. We compared alternative models by a deviance test (the difference in log likelihood between two models) that has a chi-square distribution.

A final analysis of flock fertility was based on a nonparametric technique, the Lee-Desu test statistic (Lee and Desu, 1972; SPSS, 1985). With this procedure, we tested whether ewes with different lambing numbers or mating seasons at their first mating (either as a ewe lamb or postpartum) required the same amount of time (in STAR seasons) to become pregnant. The analysis provided cumulative pregnancy rates at the end of each STAR season. These outputs were then expressed as the time (in seasons) required for 50% of the ewes to become pregnant using linear interpolation between the seasons that bracketed 50% conception. Times to pregnancy among ewes within each lambing number category were compared for each mating season, and vice versa. Because ewes left the flock at various times and data collection finished at the August 1988 lambing, data on some ewes ended before they became pregnant. Final records on such ewes were assumed to represent censored data in the calculations.

Results

Flock Performance

Means for fertility, prolificacy, lamb survival to weaning, and lamb age and weight at weaning are shown for each mating season in Table 2. Fertility was higher for matings in favorable seasons (.55) than for those in unfavorable seasons (.21). The flock was most fertile in October, although, even here, fewer than 70% of ewes lambed after a 30-d mating season. Prolificacy tended to be higher for ewes bred in favorable seasons, although prolificacy was higher for ewes bred on spring forage in June than for ewes bred

Table 2. Performance measures by mating season, or combined for favorable and unfavorable mating seasons

Item	Fertility[a]	Prolificacy[b]	Lamb survival[c]	Lamb weaning[d] Age, d	Lamb weaning[d] Wt, kg
Mating season					
January	.49	1.42	.80	60.9 ± .4	17.0 ± .2
March	.28	1.39	.86	52.6 ± .5	14.9 ± .2
June	.15	1.52	.74	52.4 ± .5	15.3 ± .3
August	.46	1.55	.82	51.3 ± .3	15.3 ± .1
October	.69	1.58	.82	57.5 ± .2	16.7 ± .1
Combined seasons[e]					
Favorable	.55	1.54	.81	55.5 ± .2	16.2 ± .2
Unfavorable	.21	1.44	.82	52.5 ± .4	15.0 ± .3

[a]Proportion of ewes lambing from this mating.
[b]Number of lambs born per ewe lambing.
[c]Proportion of lambs surviving to weaning.
[d]Mean ± SE.
[e]Favorable mating seasons were January, August, and October; unfavorable mating seasons were March and June.

in January. Across mating seasons, there was less variation in prolificacy than in fertility.

About 82% of lambs born were weaned. Only for matings in unfavorable seasons was lamb survival either elevated (86%, March) or reduced (74%, June). Weaning weights were heaviest for lambs from January and October matings. Ewes mated in these seasons conceived earlier in the mating period and their lambs were older at weaning.

The average ewe lambed .98 times/yr, gave birth to 1.50 lambs, reared 1.23 lambs, and weaned 19.6 kg of lamb/yr. After removal of fertility records made after six consecutive failures to conceive and of all fertility records of daughters of ewes born after their dam had been defined as barren, the average number of lambings per ewe (.99), number of lambs born and reared (1.49 and 1.22 lambs/yr, respectively), and weight of lamb weaned (19.3 kg/yr) changed little. Records on fewer than 200 ewes (and their daughters) were removed, so overall effects on flock performance were slight. When the records that were removed were considered alone, they differed little from those that were retained. Forty-two ewes (3.9%) lambed at five or more consecutive 7.2-mo intervals. Ten ewes lambed at seven consecutive minimum intervals and, on average, produced 10.5 lambs (2.5 lambs/yr), raised 8.1 lambs (1.93 lambs/yr), and weaned 137.9 kg of lamb within 50.4 mo (32.8 kg/yr).

Periodicities

No linear change ($P > .50$) over time was observed for fertility. Much of the variation in fertility was defined by the periodic model ($R^2 = .79$). A periodicity of 5.08 season was obtained and did not differ ($P < .10$) from an annual (five-season) periodicity. For A = 5 seasons (Figure 2), parameter estimates ($P < .01$) were .117 for $\hat{\alpha}_1$ and –.221 for $\hat{\alpha}_2$. Predicted and observed fertility aligned closely, although fertility at March and June exposures was often overestimated. The low fertility (.058) at the June 1987 exposure reflected infertility of one ram that was used heavily. The same seasonal periodicity was observed after removing ewes with extended lambing intervals; predicted and observed fertility were nearly identical to those derived from complete data.

Prolificacy increased slightly ($P < .10$) across years and seasons. After removing this trend, the periodic model accounted for a modest amount of remaining variation in prolificacy ($R^2 = .45$). Time between peak prolificacies exceeded a year (5.3 season; $P < .01$; Figure 3), suggesting that some additional unknown factors were acting to modify the expected annual periodicity in these data. Both regressors ($\hat{\alpha}_1 = -.006$; $\hat{\alpha}_2 = .128$) were important in predicting the periodicity ($P < .01$). When cycle length was fixed at five seasons, a sinusoidal function ($\hat{\alpha}_1 = .106$; $P < .01$) alone defined the periodicity. Lambings from spring and summer exposures generally produced fewer lambs, but unlike fertility, predicted and actual prolificacy rarely corresponded exactly.

Environmental Effects on Fertility

A ewe's nursing status at her previous lambing did not affect fertility ($P > .25$) whether considered alone or in combination with other fixed effects. Results of the mixed and fixed GLM were the same. Ewes that had nursed a lamb were slightly more fertile (.29) than those that had not (.25).

When ignoring nursing status, and including data from all exposures, effects on fertility of mating season, lambing number, lambing interval, and the interactions of mating season with lambing number and lambing interval were significant in both the mixed and fixed GLM. The lambing number × lambing

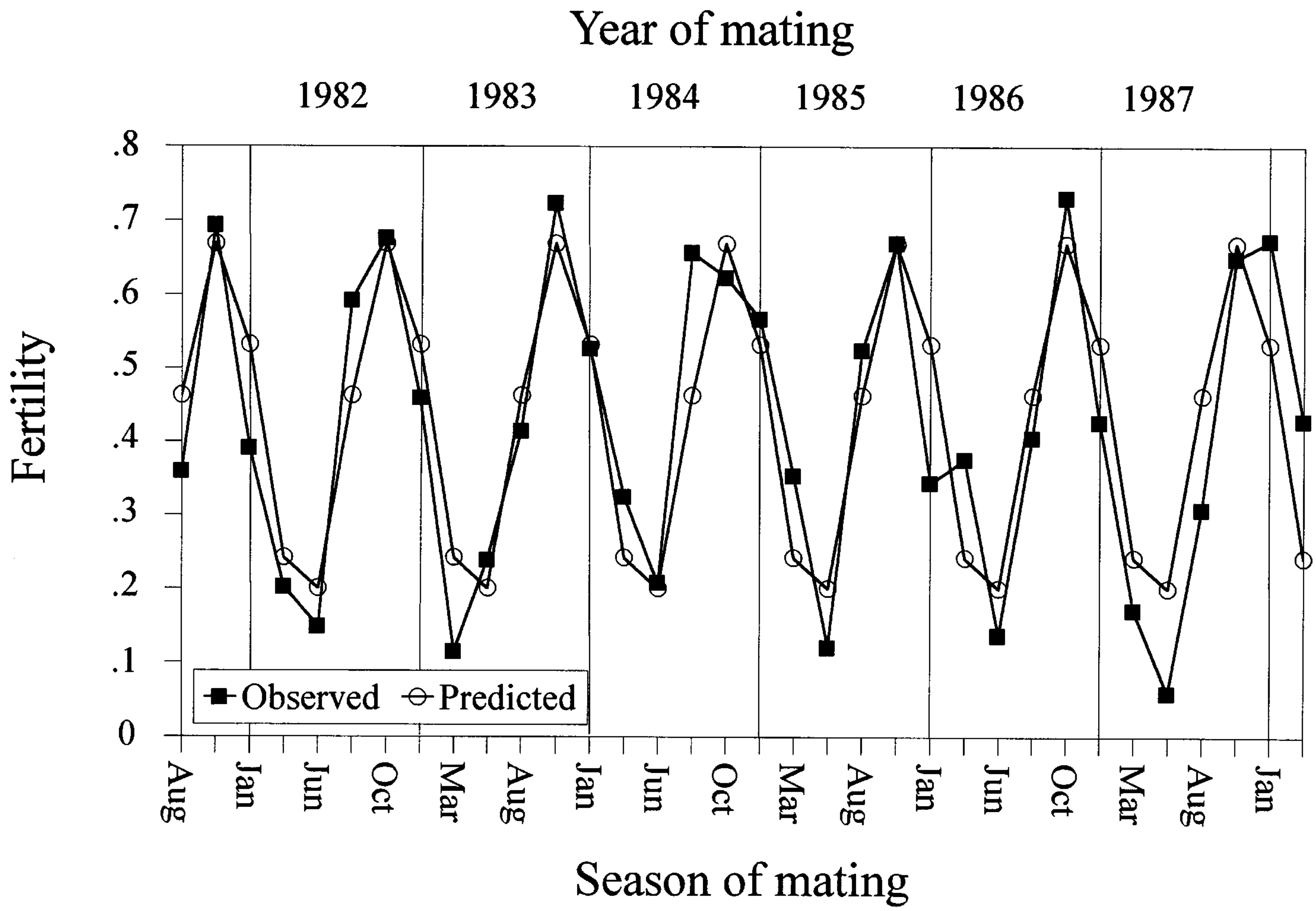

Figure 2. Observed and predicted flock fertility across years and seasons. Values are scaled to the mean fertility of the flock (.42).

interval interaction and the three-way interaction were also significant for the fixed GLM but did not reach significance for the mixed GLM ($P < .20$). Results of both analyses thus indicate that the pattern of change in fertility among mating seasons will differ for each lambing number-lambing interval combination. The estimate of residual error variance on the logit scale from the mixed GLM was 1.41 ± .06. Because the residual variance was greater than one, over-dispersion (indicative of unidentified, extra-binomial variation) was present (McCullagh and Nelder, 1989).

Table 3 presents a matrix of backtransformed probabilities of lambing from the mixed GLM with approximate 95% CI and the number of matings associated with each estimate. Each row of the matrix is a combination of lambing number and mating season. Each column is the number of intervals in STAR seasons since a ewe last lambed or, for primiparous ewes, was first exposed. Each cell in the matrix is the probability that a ewe would lamb from the mating.

The matrix traces each ewe's reproductive history in the flock. For instance, a ewe born in June would first be mated in January so her entry point in the matrix would be at the January mating, lambing number one, and lambing interval one. If she conceived to this mating, she would lamb in June and re-enter the matrix at the August mating, lambing number two. If, however, the ewe failed to conceive in January, she would move to the next diagonal element in the matrix within lambing number one, which, in this example, would be a March mating at lambing interval two.

Within the matrix, an increase in lambing number, and a diagonal movement downward within a lambing number, approximated the increase in ewe age over successive exposures. On average, ewes categorized within lambing number one, two, and three were 6.2, 10.2, 14.2 seasons old, respectively. At lambing numbers greater than three, ewes originating in the STAR system were 20.7 seasons in age and ewes originating in the CAMAL system were older at 25.9 seasons. Within each lambing number, age (in seasons) also increased incrementally as lambing interval increased.

Effects of mating season and lambing number at first exposure (lambing interval one) are summarized in Figure 4. The effects of lambing interval are shown in Figure 5 as the change in fertility from lambing interval one to two. Comparisons of lambing interval one with lambing intervals of three or more were generally similar to those in Figure 4.

Effects of mating season (Figure 4) on fertility were large and relatively consistent. In ewe lambs (lambing number one), fertility was always highest in October and was generally lowest in March or June, and fertility was higher in January than in August. Effects of lambing interval, represented as the change in fertility from lambing interval one to lambing interval two in Figure 5, were small for ewe lambs in all seasons. These results indicate that in all seasons, ewe lambs that had not become pregnant at an earlier opportunity were not less fertile than those being exposed for the first time, suggesting that early failures most likely were the result of insufficient maturity to permit successful reproduction.

Ewes were exposed for their second lambing immediately after weaning lambs and were 36 to 66 d postpartum. Fertility of these ewes at first exposure (Figure 4) was similar to that of ewe lambs in all mating seasons. However, ewes exposed in August had higher fertility at a lambing interval of two (.50; Figure 5) or greater (.53) than at a lambing interval of one (.36). Thus in August matings, longer postpartum intervals may have had a beneficial effect on fertility. A similar pattern was observed in January and June matings, whereas the pattern was reversed in October matings, but these results were based on considerably smaller numbers of observations than those available in August.

In ewes being exposed for their third lambing, fertility at first exposure (Figure 4) was higher than that observed for lambing numbers one and two in March (a time of transition between the estrus and anestrus seasons) and in October and January (the most favorable breeding seasons). However, fertility in August was only slightly higher than that observed in younger ewes, and fertility in June was lower.

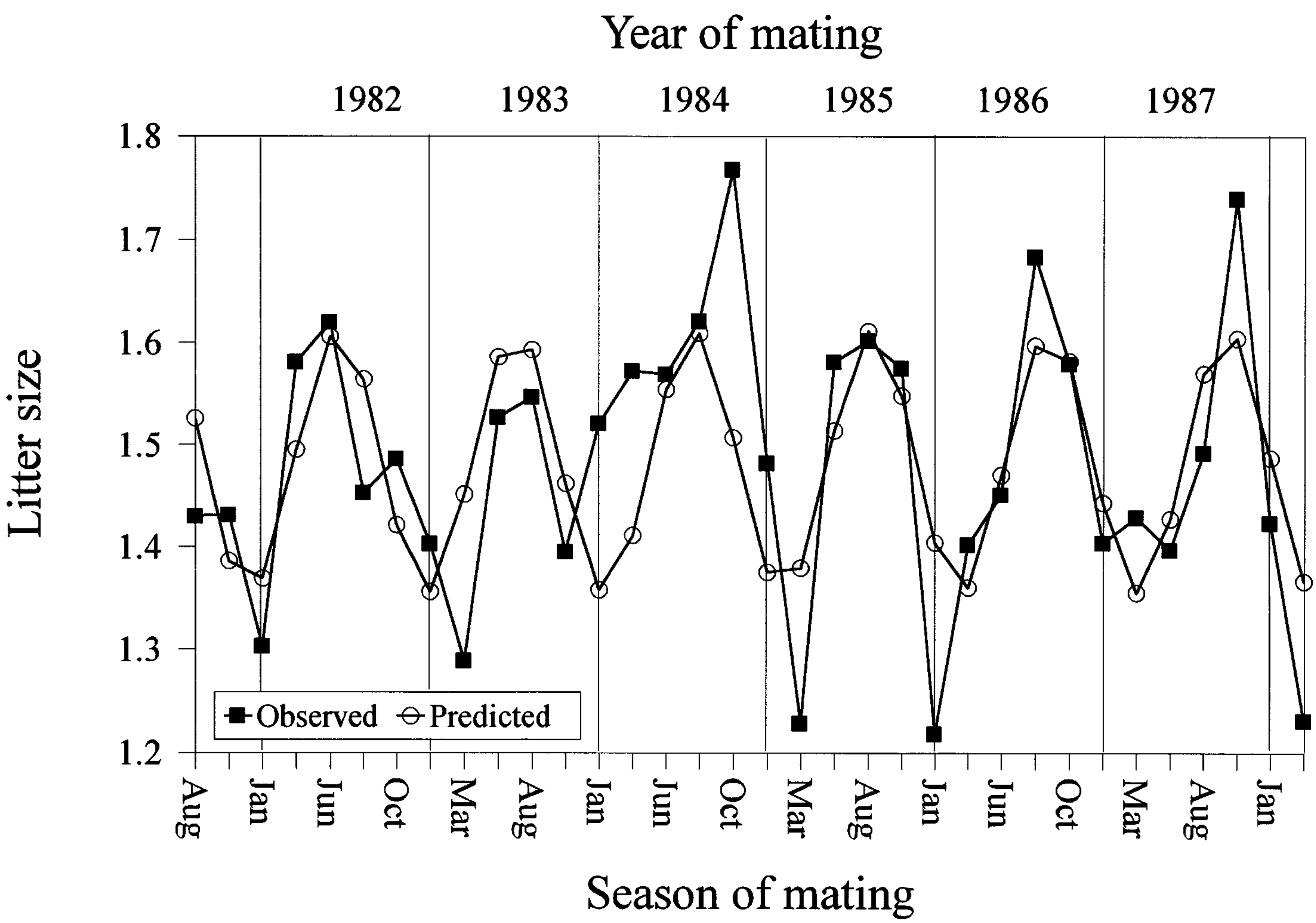

Figure 3. Observed and predicted average flock prolificacy across years and seasons. Values are scaled to the mean prolificacy of the flock (1.5 lamb born per ewe lambing).

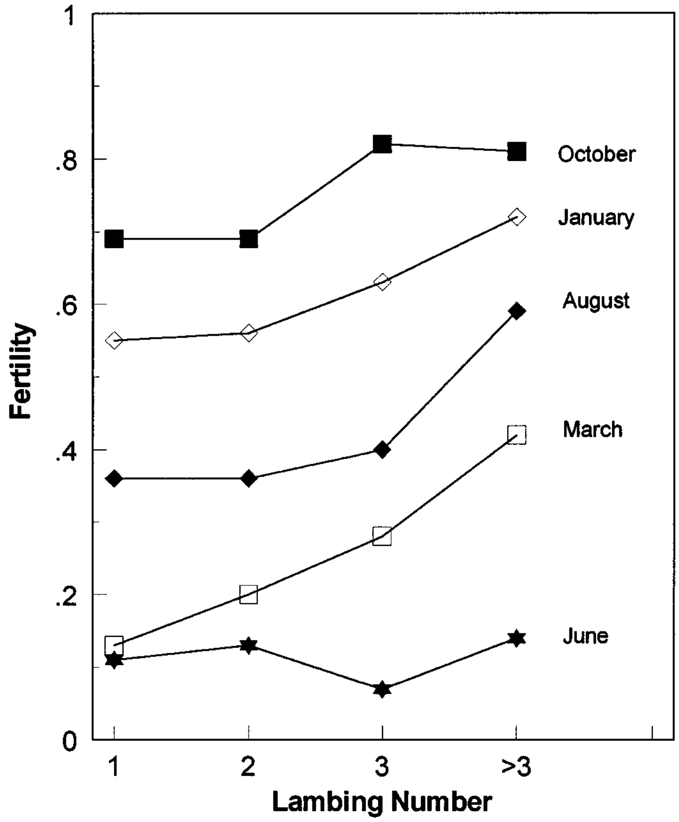

Figure 4. Fertility at first exposure by month and lambing number.

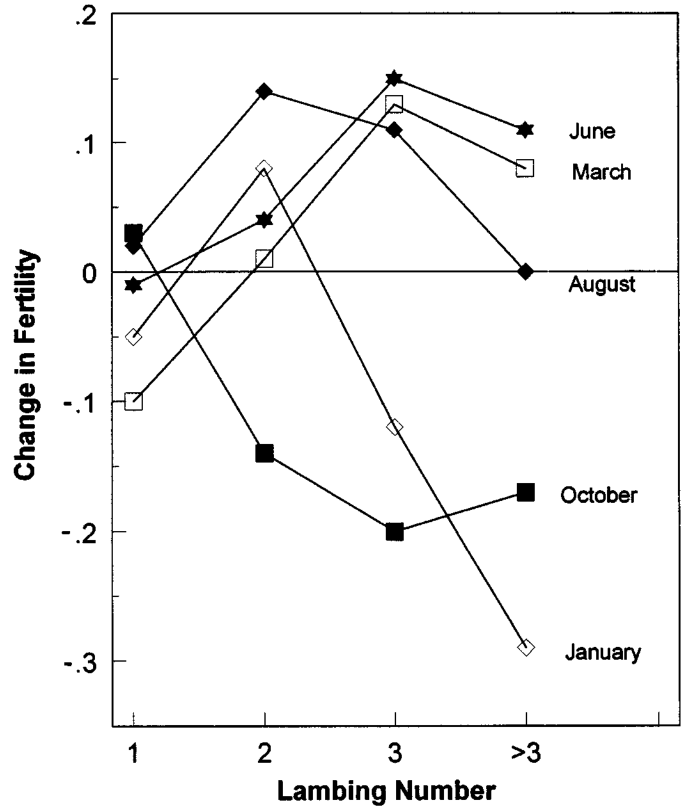

Figure 5. Change in fertility from lambing interval one to lambing interval two by month and lambing number.

Fertility in March, June, and August increased with lambing interval, whereas fertility in January and October decreased with lambing interval (Figure 5). January and October were the most favorable mating seasons and also followed relatively favorable mating seasons (August and October, respectively). In these seasons, ewes that had not become pregnant at first exposure in August or October were subsequently less fertile than first-exposure ewes. In contrast, ewes exposed in the less favorable seasons of March, June, and August seemed to benefit from additional days postpartum at second and later exposures.

In adult ewes (lambing number greater than three), patterns observed at lambing number three were accentuated. At first exposure, fertility in March, August, and January continued to increase. Fertility in October did not increase further from the relatively high level achieved at lambing number three, and fertility in June remained low. Fertility at second exposure (Figure 5) remained higher than that at first exposure for matings in March and June, but fertility at later exposures was lower (Table 3). Fertility in August was essentially unaffected by lambing interval, whereas fertility in January and October was again highest at first exposure.

In the context of modeling flock fertility during the year, interactions of mating season with lambing

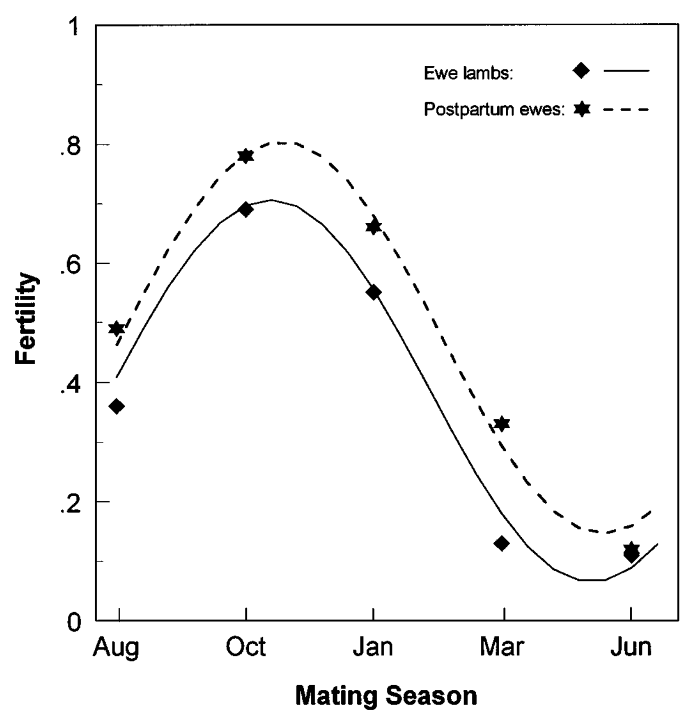

Figure 6. Observed and predicted fertility of ewe lambs and postpartum ewes mated during the year.

number and lambing interval indicate that a different pattern of annual fertility was expected for each lambing number and lambing interval. To further investigate these patterns, the periodic model (Equation 1) was applied to results shown in Table 3 to model changes in fertility among seasons for six groups of ewes: ewe lambs at their first, second, or third and greater exposure and postpartum ewes at their first, second, or third and greater exposures. Means for postpartum ewes were calculated by weighting each postpartum lambing number by its overall frequency in the data: .275, .195, and .530 for lambing number two, three, and greater than three, respectively. August was coded as mating season number one to allow comparison with results in Figure 2. The periodicity was fixed at 1 yr (A = 5).

Table 3. Predicted ewe fertility relative to lambing number, mating season, and lambing interval with subclass frequencies and 95% CI[a]

Lambing number[b] and mating season	Lambing interval[c] One	Two	≥Three
One			
January	.55 (75)	.50 (60)	.49 (87)
	.41–.69	.35–.65	.36–.62
March	.13 (107)	.03 (32)	.08 (69)
	.07–.23	.00–.26	.03–.20
June	.11 (77)	.10 (93)	.10 (85)
	.05–.22	.04–.20	.04–.21
August	.36 (286)	.38 (68)	.27 (135)
	.29–.43	.25–.53	.19–.37
October	.69 (197)	.73 (183)	.68 (120)
	.61–.77	.64–.80	.56–.77
Two			
January	.56 (21)	.64 (6)	.49 (79)
	.31–.79	.19–.93	.36–.62
March	.21 (150)	.21 (9)	.33 (29)
	.14–.30	.04–.64	.16–.56
June	.13 (297)	.17 (112)	.10 (21)
	.10–.19	.10–.28	.02–.39
August	.36 (88)	.50 (257)	.53 (99)
	.24–.49	.42–.58	.41–.65
October	.69 (20)	.55 (57)	.66 (171)
	.41–.88	.38–.70	.56–.74
Three			
January	.63 (62)	.51 (6)	.38 (38)
	.47–.76	.13–.88	.21–.57
March	.28 (196)	.41 (21)	.42 (12)
	.21–.37	.19–.67	.15–.75
June	.07 (83)	.22 (111)	.30 (13)
	.03–.18	.14–.33	.09–.65
August	.40 (27)	.51 (77)	.57 (94)
	.21–.63	.37–.64	.44–.69
October	.82 (40)	.62 (16)	.60 (78)
	.63–.92	.32–.85	.47–.73
≥Four			
January	.72 (117)	.43 (33)	.26 (56)
	.60–.81	.24–.63	.14–.42
March	.42 (380)	.50 (30)	.32 (44)
	.35–.48	.29–.70	.18–.51
June	.14 (278)	.25 (197)	.10 (31)
	.10–.20	.18–.33	.02–.32
August	.59 (142)	.59 (237)	.57 (164)
	.49–.69	.51–.67	.47–.66
October	.81 (198)	.64 (56)	.74 (157)
	.74–.87	.48–.78	.64–.81

[a]Probabilities were back-transformed from logistic means. For each subclass, probabilities and subclass frequencies (in parentheses) are shown on the first line. The 95% CI is shown on the second line.

[b]Number of previous lambings + 1.

[c]Lambing interval one indicates the first exposure for ewe lambs or the first exposure after lambing for older ewes. Lambing intervals of two or more represent ewes that had failed to conceive at one or more prior opportunities.

Values for $\hat{\alpha}_1$, $\hat{\alpha}_2$, and R^2 in ewe lambs were .120, –.297, and .99 for first exposure, .185, –.304, and .97 for second exposure, and .117, –.295, and .95 for later exposures. For postpartum ewes, comparable values were .089, –.317, and .99 for first exposure, .083, –.154, and .82 for second exposure, and .164, –.173, and .76 for later exposures. Parameter estimates were generally consistent with values of $\hat{\alpha}_1$ = .117 and $\hat{\alpha}_2$ = –.221 obtained using observed year-season means in Figure 2. Predicted fertility of ewe lambs was similar across lambing intervals; results for first exposure are shown in Figure 6. The R^2 values for ewe lambs were consistently high, whereas accuracy of prediction of postpartum fertility was high at first exposure (Figure 6) but declined at later exposures (not shown). Poorer predictions at later exposures for postpartum ewes presumably relate to the greater number of factors that can affect fertility in these ewes.

The time required for a ewe to become pregnant is shown in Table 4 relative to the season in which the ewe was first mated and her lambing number. Time to pregnancy varied with season of first mating ($P < .05$) and lambing number ($P < .001$). Time intervals were longer when ewes were first mated in an unfavorable season (March or June). This result was particularly evident for March matings, because ewes that failed in March were next mated in June. The time interval until pregnancy was longer for August than for January matings, although the difference was small ($P > .05$). As ewes aged, the time to pregnancy shortened ($P < .05$). The shortest intervals to pregnancy were for ewes at their fourth or later lambing.

Discussion

Within and across years, fertility followed a consistent annual periodicity with conception rates higher in autumn and winter (October through January) and lower in spring (March and June). Ovarian and estrous activity in Dorset ewes have been shown to follow a similar pattern (Phillips et al., 1984; Hall et al., 1986). In these data, approximately 20% of ewes exposed in spring conceived. Such reduced conception rates during spring have consistently been reported in Dorsets and other breed types (Whiteman et al., 1972; Notter and Copenhaver, 1980; Fogarty et al., 1984; Iniguez et al., 1986). Although Dorsets are considered a desirable breed for accelerated lambing because they tend to have an extended breeding season (Dufour, 1974), clearly they exhibit enough seasonality to restrict performance in such programs.

Season also influenced prolificacy. Both prolificacy and fertility were highest for October matings, whereas in other seasons, rankings for prolificacy and fertility did not correspond. Ewes that conceived in March were less prolific than those that conceived in other seasons, but prolificacy from June matings, despite poor fertility, was similar to that in August and higher than that in January. Notter and Copenhaver (1980) and Fogarty et al. (1984) also reported asynchrony in prolificacy and fertility in pure and composite breeds allowed to lamb three times in 2 yr. In those studies, fertility and prolificacy were both higher at matings during the normal breeding period (August and either November or December) than during the anestrus period (April). But, within the normal breeding period, months of maximum fertility and prolificacy did not correspond. The highest prolificacy was observed at August matings by Fogarty et al. (1984) but at November matings by Notter and Copenhaver (1980). Thus, seasonal influences cause variability in reproductive rate in frequent lambing systems that seems linked to the management calendar and breeds chosen.

Fertility at first exposure (Figure 4) depended on both ewe age and mating season. Fertility within each mating season was similar in ewe lambs and in ewes

Table 4. Time interval (in STAR seasons) required for 50% of the ewes to become pregnant by season of first exposure and lambing number[a]

Season of first exposure	Lambing number				Lee-Desu statistic[bc]
	One	Two	Three	≥Four	
January	1.4^{er}	1.4^{eq}	1.3^{deq}	1.2^{dq}	13.0**
March	3.7^{ft}	2.9^{es}	2.6^{es}	1.9^{ds}	72.8***
June	2.6^{es}	2.4^{er}	2.4^{des}	2.2^{dt}	10.5*
August	1.8^{et}	1.9^{eq}	1.5^{der}	1.4^{dr}	19.4***
October	1.2^{eq}	1.4^{eq}	1.1^{dq}	1.1^{dq}	11.7**
Lee-Desu statistic[bc]	130.2***	22.8***	66.4***	193.7***	—

[a]An interval of one would indicate that a ewe lambed when mated at the specific season. Tabular values were derived by linear interpolation between seasons to the point of 50% conception.

[b]Test statistics shown down the columns refer to comparisons between mating seasons within a lambing number. Test statistics shown across the rows refer to comparisons between lambing numbers within a mating season. Due to unequal subclass numbers, differences of the same absolute size may, or may not, always be significant.

[c]Significance levels: *$P < .05$; **$P < .01$; ***$P < .001$.

[d,e,f]Values within a row lacking a common superscript differ ($P < .05$).

[q,r,s,t]Values within a column lacking a common superscript differ ($P < .05$).

being exposed for their second lambing. At later exposures, fertility in October had increased to a maximum following the second lambing, whereas fertility in January, August, and March continued to increase with ewe age. Fertility in June was uniformly low and unresponsive to increasing ewe age. An increase in fertility with increasing ewe age was reported by Dickerson and Glimp (1975) and Notter and Copenhaver (1980). Iniguez et al. (1986) found season of birth effects ($P < .05$) in Dorset ewes first lambing at under 2 yr of age and managed in either CAMAL or continuous lambing. Ewes born in summer and first exposed to rams the next winter or spring at 6 to 12 mo of age had much lower fertility than ewes born in winter and fall and first mated in the subsequent summer.

The effect of increasing age in ewe lambs (lambing number one) on fertility was small in all seasons, whereas effects of increasing days postpartum were larger and varied among seasons (Figure 5). Postpartum fertility in June and March was always higher for ewes that had an additional season (73 d) to recover from lactation. This result was observed in August only after the first and second lambing and was observed in January only after first lambing. Ewes that were exposed in October that had failed to conceive in August were consistently less fertile than ewes exposed in October that had just weaned lambs, indicating that additional days postpartum were not important in fall breeding.

The number of lambs nursed by a ewe at the lambing preceding her current exposure did not affect her fertility. Small effects of prolificacy at the preceding lambing on conception rate have been reported elsewhere. Iniguez et al. (1986) reported that ewes producing singles required 11 more days to conceive than ewes nursing more than one lamb, but the effect was not significant. Notter and Copenhaver (1980) found that increasing time since last lambing had a significant negative effect on fertility in April.

A complex array of environmental effects combined to control fertility in the STAR system. Thus, an integrated approach to account for these effects seemed appropriate. The probability matrix incorporated those factors with greatest bearing on fertility (mating season, lambing number, and lambing interval). The time interval before a ewe conceived differed for each lambing number ($P < .001$) and previous season of lambing ($P < .05$). Thus, the dimensions of the matrix of transition probabilities shown in Table 3 were likely the minimum required to describe environmental effects on fertility in the STAR system.

Residual variance in fertility was greater than expected for binomial variation alone, as indicated by the over-dispersion noted earlier (McCullagh and Nelder, 1989). This result suggests that other environmental factors not included in our model may contribute to ewe fertility. One source of extra variation may be the assumption of independence among observations. A ewe's birth and lambing season determined the first season in which she was mated. If a ewe failed to conceive to that mating, she was exposed again the following season, and carry-over effects not accounted for by the model may have existed. Although the model provided a biologically sensible description of fertility, further refinements may be possible.

The lambing frequency among these Dorset ewes managed in the STAR system was less than in other accelerated lambing programs. On average, ewes lambed once yearly. Iniguez et al. (1986) reported annual lambing rates among Dorset ewes of 1.21 lambings/yr for ewes managed in the CAMAL system and 1.33 lambings/yr for ewes under continuous exposure. In CAMAL, spring matings occurred in April and June. When mated three times in 2 yr with the seasonal exposure in April, crossbred ewes were reported to lamb 1.27 times annually (Notter and Copenhaver, 1980). Walton and Robertson (1974) reported that a small flock of Finnish Landrace ewes mated twice yearly over 2 yr lambed 1.60 times annually; however, these ewes' out-of-season mating occurred between mid-January and late April and most ewes conceived by early spring. In our data, the extremely low fertility observed in June for ewes of all ages (14% and below at lambing interval one) contributed to their relatively lower productivity. Further, even at October exposures where fertility was greatest, fewer than 82% of the ewes conceived. In a flock of inherently higher fertility or if the orientation of the STAR were rotated to avoid mating during a month of low fertility (June in this flock), production levels could perhaps have been improved. However, a few individuals within the flock were capable of lambing on a regular basis throughout the year.

Implications

Fertility and prolificacy in the STAR accelerated lambing system varied systematically among seasons during the year. Fertility was controlled by a complex interplay of effects of ewe age (expressed as lambing number), mating season, and time since last lambing. A matrix showing expected fertility levels was constructed and can be used to predict fertility for various types of ewes exposed in different seasons of the year. Values in the matrix can also be used to adjust fertility data and(or) form contemporary groups in programs for genetic evaluation of reproductive traits in accelerated lambing systems.

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