REPRODUCTIVE PERFORMANCE OF DORSET EWES IN
THE STAR ACCELERATED LAMBING SYSTEM

by

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(ABSTRACT)

Reproductive performance of Dorset ewes in the Cornell University STAR accelerated lambing program was evaluated. This program consists of five 30-d concurrent breeding and lambing periods per year beginning on January 1 (S1), March 15 (S2), May 27 (S3), August 8 (S4) and October 20 (S5). Optimally, a ewe could lamb every 7.2 mo beginning at 1 yr of age. Records on 1,084 ewes over 7 yr beginning S1, 1982 were used. Reproductive traits considered were ewe fertility, prolificacy, days to first lambing (DFL) and days between lambing (DBL).

Fertility and prolificacy differed (P < .001) by exposure seasons. Exposure during favorable seasons (S1, S4, S5) increased fertility (P < .001) and prolificacy (P < .01) over that observed in unfavorable seasons (S2, S3). On average, first lambing occurred at 476 ± 5 d with ewe lambs first exposed during S1, S4 and S5 lambing at younger ages (P < .001). Ewes had more DBL (P < .001) if initial exposure following lambing occurred during an unfavorable

season.

A curvilinear relationship of ewe age with fertility (P < .001), prolificacy (P < .01) and DBL (P < .05) was observed in ewes less than 4 yr old. At first exposure following lambing, fertility was lower (P < .001) than at subsequent exposures and ewes that had nursed lambs were less prolific (P < .01) than those that had not. Prolificacy and nursing status had little effect on fertility or DBL (P > .10).

Fertility was transformed to an underlying liability scale based on the expected fertility of ewes of a given age and reproductive history. Variance components were estimated by least-squares (LS) and restricted maximum likelihood (REML) procedures. First-exposure fertility was not heritable. Heritabilities for fertility at first post-lambing exposure, first-lambing prolificacy, and second-lambing prolificacy were .191 ± .088 (LS) and .200 ± .132 (REML), .194 ± .091 (LS) and .158 ± .144 (REML), and .168 ± .082 (LS) and .210 ± .137 (REML), respectively. Genetic variation in DFL (P < .01) and DBL (P < .001) was found. Although intrasire ewe variation was detected for prolificacy (P < .001) and DBL (P < .01), repeatability estimates were low and smaller then heritability.

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Table of Contents

Tables

Figures

Literature Review

Reproductive rate can be defined as the number of lambs weaned per ewe exposed to a ram. Although Turner (1969) suggested ten discrete factors as components of reproductive rate, generally three main categories have been identified (Shelton and Menzies, 1970): fertility within a given year (either a ewe lambed or failed to lamb), prolificacy for a given lambing (the number of lambs born), and livability for a given birth (either a lamb was weaned or not weaned). In combination, these categories determine the total number of lambs that can be marketed. A lamb's weaning weight is closely related to its sale value. Thus the live weight as well as number of lambs marketed affect production efficiency (Shelton and Campbell, 1962).

The profitability of lamb production could be enhanced by increasing prolificacy and fertility. In extensive production systems, forage and management resources restrict alternatives for improving lamb production to increased prolificacy at an annual lambing. Under intensive management, an array of accelerated or multiple-season lambing systems provide additional opportunities to optimize lamb production. Most breeds exhibit an anestrous period between March and July, thereby restricting flexibility in designing accelerated programs. Extension of the estrous period would allow more opportunities for increasing lambing

1

incidence.

Reproductive performance can be modified in two fashions: by improvements in the environment (management, feeding, etc.) and by the use of genetic differences between breeds and individuals (Turner, 1969). Since genetic improvement provides more permanent gains in performance, it may be considered of relatively greater long-term importance (Shelton and Menzies, 1968; Turner, 1969; Land, 1981). Yet the expression of genetic merit is affected by environmental factors. A knowledge of the relationship between the environment and an animal's genotype is thus useful in a breeding program.

Environmental Effects on Annual Reproduction

Reproductive traits are strongly affected by the environment. Depending on the age, birth type, nutritional status and condition of a ewe, her reproductive rate may vary each year. In order to identify animals with superior genetic merit for reproductive traits, it is essential to understand the environmental contributions enhancing or detracting from performance.

Considerable research on environmental effects on reproduction in annual lambing systems has been conducted. Before focusing on accelerated lambing programs, a survey of these investigations in annual systems seemed prudent.

Age. For most breeds and localities, fertility and prolificacy increase with age up to 6 yr and then decrease. Turner and Dolling (1965) found that the proportion of ewes failing to lamb fell from 18% for 2-yr-olds to 8% for 5- to 6-yr olds. The proportion of infertile ewes again rises to 14% for ewes 10 yr of age. Dickerson and Glimp (1975) examined seven domestic breeds and noted that fertility and the number of lambs born per ewe increased curvilinearly with the age of the ewe. Their studies indicated that 50 to 80% of 1- or 9-yr-old ewes produced a lamb compared to 85 to 95% of 4- to 6-yr-old ewes. Yearling ewes produced a 100+% lamb crop which increased to 160% as 6-yr-olds and dropped back to 135% for 9-yr-olds. Eikje (1971) indicated that a maximum in the number of lambs born was reached when ewes were 5 to 7 yr of age and such ewes produced .8 to .9 more lambs than yearling ewes. When the number of lambs born per ewe joined was considered, Turner and Dolling (1965) observed a rise from a minimum of 84% for 2-yr-olds to a maximum of 111% for 7-yr-olds. Although lambs born per joining fell to 104% for 10-yr-old ewes, the figure exceeded that for ewes 2 to 4 yr of age. Reeve and Robertson (1953) suggested that flocks with higher average prolificacy reached a maximum production level at an earlier age and then declined in performance when compared with flocks with lower maximum litter size. Both breed and maximum production level thus complicate the relationship between

prolificacy and age.

Type of birth. The relationship of birth type with reproductive rate is unclear. Vakil et al. (1968), working with fine- and medium-wool breeds, found that ewes born as twins tended to produce more offspring than those born as singles. A considerably higher fertility of twin as compared to single-born Australian Merino ewes was reported by Dun and Grewal (1963). Piper and McGuirk (1976) suggested that several lambings may be required before twin-born Australian Merino ewes demonstrate their superiority in reproductive rate (combined fertility and prolificacy). In the South African Merino, van der Westhuysen (1973) estimated that twin-born ewes produced .04 more lambs over their lifetime than single-born ewes, a nonsignificant difference. Twin born ewes have not uniformly been found to be superior in reproductive performance. In the Romney, twin-born ewes produced fewer offspring than single-born ewes (Wallace, 1964). Baharin and Beilharz (1977) indicated that Corriedale ewes born as twins had both reduced fertility at first mating and an earlier decline in reproductive rate with increasing age.

Body size and nutrition. Ovulation rate can be considered a threshold trait. Depending on the number of ova shed, a ewe has the potential of producing zero, one or more lambs from a given breeding. Live weight or body size appear strongly correlated with ovulation rate and litter

size (Ray and Smith, 1966; Dyrmundsson, 1973; Hohenboken et al., 1976). Foote et al. (1959) reported that up to some optimum, ewes with a higher body fat content and greater size at breeding had higher ovulation rates. Flushing or temporarily increasing the plane of nutrition prior to breeding is a common management technique intended to increase the lamb crop (Cumming, 1977).

Several studies have been conducted to quantify the effect of flushing. Reeve and Robertson (1953) noted an increase from 128.7 to 147.7% in the lamb crop as the result of flushing. Ewes that gained the most weight also produced more sets of twins. They also suggested that flushing may increase ovulation only in thin ewes. Ewes in good body condition preceding flushing may show no ovulatory response to the additional feed. Fletcher (1971) reported no response to flushing in South Australian Merino ewes that were 5 and 6 yr of age. Foote et al. (1959) observed a variable response to flushing. The practice increased ovulation rate in adult ewes but had only marginal effects on 2-yr-old ewes. Flushing had no effect on ewe lambs. The total body growth of the lamb appears more important in stimulating sexual maturity and ovulation rate than a short flushing period (Foote et al., 1959; Dyrmundsson, 1973).

Differences in ovulation rate between groups of ewes may best be explained by differences in body weight at breeding (Foote et al., 1959). Hohenboken et al. (1976)

identified a slightly higher prolificacy among ewes grazing irrigated as compared to hill pasture. The ewes on irrigated pasture weighed approximately 2.0 kg more than ewes on hill pasture. They also reported a negative relation between increases in body weight and prolificacy during the breeding season. Fletcher (1971) observed a 1.3% increase in the incidence of twin ovulations for each 1.0 kg difference in liveweight at breeding.

Puberty. Early sexual development may be an indication of increased fertility in ewes. Range ewes that cycle as yearlings tend to be more prolific and to rear heavier lambs throughout their lifetime (Dyrmundsson, 1973). Holland and Ruttle (1966) concluded from records on three lamb crops that the total number of lambs weaned will be greater from those ewes first lambing at 1 yr. Lambing as a yearling did not seem to depress subsequent performance.

The genetic contribution to the age of puberty tends to be hidden by environmental effects. Foote et al. (1959) noted that yearling ewes supplemented with grain for 6 mo preceding breeding had increased ovulation rates. The increased ovulatory activity was attributed to an increased body weight at breeding. Holland and Ruttle (1966) and Dyrmundsson (1973) reported that body weight and sexual maturity in lambs were closely related. Land (1978), on the contrary, suggested that "genetic and environmental variation in puberty" may be independent of that in body

growth. Non-supplemented Blanche de Lozere and Scottish Blackface females, which cycled as yearlings, were not significantly different in body weight than those failing to show estrus. Supplemented lambs of both breeds cycled more readily than non-supplemented lambs (Land, 1978).

A disadvantage of ewes maturing and breeding at an early age may be a reduction in fleece production. Holland and Ruttle (1966) state that ewes lambing as yearlings produced .3 kg less clean fleece weight than those which failed to lamb. The reduced fleece production may result from the added stress of raising a lamb or could be inherent to rapidly maturing females (Holland and Ruttle, 1966).

Season. Reeve and Robertson (1953) indicated that fertility varies considerably within a breeding season and between breeds and regions. Generally, ovulation rate increased through the middle of the breeding season and then declines (Reeve and Robertson, 1953; Hohenboken et al., 1976). Cumming (1977) failed to observe the expected rise in ovulation rate associated with increased body weight early in the breeding season. As the breeding season progressed, ovulation rate increased for a given change in live weight. The frequency of multiple births from ewes settled later in the breeding season is often considered to be higher (Reeve and Robertson, 1953; Hohenboken et al., 1976).

Environmental Effects on Accelerated Lambing

Accelerated lambing programs are designed to increase the incidence of lambing per ewe per year. In addition to the increased reproductive efficiency that may be achieved with frequent lambing systems, Hogue (1986) suggested that a more uniform supply of lamb, an increased utilization of facilities and forages and a more uniform cash flow to the producer were other advantages of these systems.

In most research concerning accelerated lambing, reproductive performance has been characterized using at least one of four traits. Unsurprisingly, ewe fertility, particularly at seasons of reduced sexual activity, and prolificacy have received the most attention. Age at first lambing and lambing interval (the number of days between consecutive lambings) have also routinely been used to define performance in frequent lambing systems.

Continuous lambing.

Three general types of accelerated programs have received attention in the literature. Continuous lambing will be considered first. In continuous lambing systems, males remain with females throughout the year (Gabina, 1989a) allowing lambs to be born year-around. The Cornell alternate month accelerated lambing (CAMAL) system (Hogue et al., 1980; Iniguez et al., 1986) approximates a continuous

program since breedings and lambings occur in alternate months, allowing for average lambing intervals of 6, 8, 10 and 12 mo.

Ewe fertility. Seasonal effects on fertility in continuous systems are apparent. Terrill and Lindahl (1975) reported that the lowest numbers of live lambs were born in July, August and September (7%) and the most were born from October through March (77%) in Rambouillet crossbred ewes. Similar reductions in fertility during exposures in periods of typically low sexual activity in Dorsets were reported by Iniguez et al. (1986).

Age at first lambing. Iniguez et al. (1986) considered season of birth effects on age at first lambing among ewes managed in a continuous lambing system and in CAMAL. Dorset ewes born in fall and winter tended to lamb at younger ages than ewes of the same breed born in other seasons. This reflects an interaction of birth season and early exposure seasons since fall- and winter-born lambs, when exposed during seasons of better reproductive activity, would be younger than spring- and summer-born lambs. Precocious ewe lambs in continuous systems tend to be less prolific (Iniguez et al., 1986).

Lambing interval. Lambing interval has been suggested as a measure for evaluating reproductive rate in continuous lambing systems (Gabina, 1989a). Iniguez et al. (1986) and Gabina (1989a) found that lambing interval was controlled by

the season in which the previous lambing occurred. Intervals were longest following winter lambings in association with reduced estrus activity in the spring. Terrill and Lindahl (1975) noted a tendency within ewes for shorter intervals to be followed by longer ones and vice versa. Prolificacy at previous lambing had a negligible effect on interval (Iniguez et al., 1986). Iniguez et al. (1986) observed an increase of about 4.4 d per year in interval length as ewes aged.

Notter (1989) found that continuous exposure of nonpregnant Dorset crossbred yearling ewes to vasectomized rams during the anestrous period prolonged time to first mating by 6 wk as compared to gestating ewes isolated from rams until parturition. This would suggest that in continuous lambing systems, lambing frequency may be depressed by continual ram exposure. Among sheep in Spain (Valls Ortiz, 1983), a higher lambing incidence and prolificacy were realized when ewes were isolated from rams at least bimonthly.

Twice-yearly lambing.

With a mean gestation length of 144 to 147 d, it is possible for ewes to lamb twice per year provided they conceive within 35 to 38 d postpartum. Very few ewes, even those selected from the most nonseasonal breeds, however will achieve this level of production (Hogue et al., 1980).

Ewe fertility. Walton and Robertson (1974), working with Finnish Landrace ewes in Eastern Canada, reported that 72% of ewes exposed conceived at three consecutive 6 mo intervals. Conception rates for both first breeding of ewe lambs and adult ewes were high during fall (84 to 100% conception). Conception rate at spring breeding was considerably lower. Similar finding were reported for Polypay, Dorset, St. Croix and Targhee ewes (Pope et al., 1989); postpartum ewes took longer to rebreed in spring than in fall. Among Dorsets, Rambouillets and their cross, only 34% became pregnant at spring breeding as compared to 84% in the fall (Whiteman et al., 1972). Of the ewes that lambed during fall, 82% mated following lambing with an average interval to mating of 32 d. For spring-lambing ewes, 50% mated and the average interval to mating was 59 d. Apparently, ewes resumed cycling earlier during the fall and a greater number exhibited estrus.

Prolificacy. Adult ewes are more prolific than lambs although prolificacy in fall and spring did not differ (Walton and Robertson, 1974). Whiteman et al. (1972) reported a higher prolificacy as well as fertility for spring-lambing Dorset and Rambouillet ewes. Prolificacy and the number of lambs a ewe nursed had no residual effect on subsequent lambing interval.

Lambing three times in 2 years.

When ewes are given the opportunity to lamb every 8 mo, breeding and lambing seasons occur at 4 mo intervals. Variants of the system have been proposed in which ewes are bred to lamb every 7 to 9 mo to allow ewes lambing out of season more time to rebreed than ewes lambing in season (Notter and Copenhaver, 1980).

Ewe fertility. Notter and Copenhaver (1980) detected differences in conception rate between Finnish Landrace crossbred ewes and Suffolk X Rambouillet crossbred ewes in August (90%), November (79%) and April (53%) with three lambings per 2 yr. Fertility was similar across breeds except in April when 1/2-Finnish Landrace ewes were more fertile then 1/4-Finnish Landrace and Suffolk-cross ewes. Fogarty et al. (1984), working with a variety of purebred and crossbred ewes, found even greater seasonal differences in fertility, with a low of 17% for April breedings. In Spain, Aragonesa ewes showed little variation in fertility across seasons (Valls Ortiz, 1983; Gabina, 1989a) although lambings dates were delayed with exposures during aseasonal months.

Age effects on fertility appear most pronounced during anestrous seasons. Gabina (1989a) noted a 10 to 14% reduction in fertility among 2-yr-old as compared to mature ewes exposed between March and June. Notter and Copenhaver (1980) reported a gradual increase in conception rate as

ewes aged until 5 to 6 yr.

Gabina (1989a) reported higher fertility among Aragonesa ewes at the exposure immediately following lambing than at later seasons and suggested that ewes failing to rebreed quickly are habitually less fertile. Litter size at the preceding lambing had little effect on fertility. Notter and Copenhaver (1980) observed a 3 to 5% reduction in conception rate (P < .40) among Finnish Landrace crossbred ewes exposed in August or November within 2 to 4 mo after lambing vs ewes exposed at 7 mo post-lambing. Conversely, at April exposure, ewes with shorter intervals had a 23% higher conception rate. Fogarty et al. (1984) noted that a 8-mo vs 12-mo lambing interval significantly reduced fertility (52 vs 65%) in several pure and composite breeds, particularly when subsequent exposure occurred in May.

Prolificacy. Season of lambing has a marked influence on litter size. Matings in autumn result in higher levels of prolificacy than in other seasons (Gabina, 1989a). Notter and Copenhaver (1980) reported a .62 decline in prolificacy between April and September. Season of maximum conception rate and prolificacy, however, did not correspond; conception rates were higher in January than April although the opposite was true for prolificacy. They observed considerable seasonal variation in prolificacy among the breeds considered. Fogarty et al. (1984) reported prolificacies of 1.93, 1.83 and 1.49 for lambings in

January, May and September, respectively. Prolificacy tends to increase quickly at young ages stabilizing at 4 to 6 yr (Notter and Copenhaver, 1980; Gabina, 1989a).

Age at first lambing. Gabina (1989a) noted greater sexual precocity in Aragonesa flocks managed for three lambings in 2 yr than in those with continuous lambing. He suggested that this superiority was the result of the "ram effect", the induction of estrous when non-cycling ewes previously isolated from males are commingled with rams (Martin et al., 1986).

Birth type and season of birth affect age at first lambing; ewes born in multiple litters or in seasons leading to first exposure during periods of reduced sexual activity tend to be older at first lambing (Gabina, 1989a). Young age at first lambing does not shorten the productive life of ewes. Gabina (1989a) found no correlation between age at first lambing and prolificacy at fixed ages across a ewe's lifetime.

Lambing interval. As with fertility, age effects on lambing interval appear restricted to anestrous seasons. Younger ewes tend to have longer intervals (Gabina, 1989a). Lactational anestrous is often considered a barrier to rebreeding shortly following lambing. Valls Ortiz (1986), working with Aragonesa and Manchega ewes, suggested that lambing interval would be prolonged only if the ewe was lactating just before exposure in unfavorable seasons.

Notter (1989) observed no delay in mating among ewes exposed to vasectomized rams immediately following lambing. In ewes allowed a 40-d lactation period, days to conception was delayed in Dorset, Polypay, St. Croix and Targhee ewes (Pope et al., 1989). However, lactation only delayed the date of first ovulation in spring.

Genetic Effects on Reproduction

Both the fertility and prolificacy of a ewe influence its reproductive efficiency. In a breeding program, prolificacy may better lend itself to improvement through selection. McBride (1958) and Turner (1966) noted that in annual lambing programs selection for twinning rather than against barrenness is a more efficient means to improve reproductive rate. Ewes selected for a history of twinning at 5 to 6 yr of age produced 35% more multiple births in their next four lambings than ewes selected for bearing singles at the same age (Turner, 1966). Turner (1966) showed a distinct correlation between prolificacy at lambings early in a ewe's life to those in later life. An initial litter size of one vs two lambs was associated with a greater increase in prolificacy in later lambings than an initial litter size of zero vs one lamb.

Repeatability. Phenotypic improvement from selection within a generation depends on the repeatability of a trait

(Turner, 1966). In general, repeatability estimates for reproductive traits are low. Reported values for the repeatability of prolificacy in annual lambing systems range from 0.04 to 0.24 (Johansson and Hansson, 1943; Rendel, 1956; Purser, 1965; Inskeep et al., 1967; Turner, 1969; Shelton and Menzies, 1970; Eikje, 1975). Turner (1969) noted that repeatabilities for litter size were often higher than those for other reproductive traits. Shelton and Menzies (1970), studying the fertility of ewes in the Edwards Plateau region of Texas, reported negative values for repeatability. These findings suggest that under conditions of suboptimal nutrition, there may be a tendency for alternate-year lambing. They concluded that the successful raising of one or more offspring in a given year may, in fact, adversely influence a ewe's ability to reproduce the subsequent year, causing oscillation between successive parities. In the same light, repeatability values for litter size based on first and second lambings at 2 and 3 yr of age, respectively, are generally lower than estimates based on lambing records of ewes of older ages (Purser, 1965). Purser (1965) suggests that yearling ewes may have more difficulty carrying and raising twin lambs than mature ewes. Shelton and Menzies (1970), recognizing that the frequency of multiple births increases with age, reported that ewes which are more prolific at younger ages do tend to produce larger litters throughout their produc-

tive life.

In a three time in 2 yr lambing program (Notter, 1981) involving crossbred Finish Landrace ewes, repeatability estimates of conception rate across seasons varied between .08 and .13. When data on eight consistently barren ewes were removed, between-ewe variation was reduced and repeatabilities became smaller. For specific lambing seasons (January, April and September) repeatability of conception rate was only significant for September lambings (.19) which corresponds with out-of-season exposure. Gabina (1989b) reported a repeatability of essentially zero for fertility in all mating seasons for Aragonesa flocks in a similar frequent-lambing system. In continuously lambing flocks, the repeatability of lambing interval (.10 to .16) was significant only when exposure occurred in unfavorable seasons.

Repeatabilities of litter size in frequent-lambing systems were larger than for fertility. Ewe effects on prolificacy were significant in all seasons in a three times in 2 yr lambing system, although highest at April lambing (.38; Notter, 1981). In Aragonesa ewes, repeatabilities for litter size were between .08 and .19 (Gabina, 1989b).

Heritability. The heritability of a trait indicates how efficient selection will be in improving future generations (Young et al., 1963). In annual lambing systems heritability estimates for prolificacy are generally low.

Heritability values may be based on single or multiple lambing records, the later estimates tending to be higher (Johansson and Hansson, 1943; Rendel, 1956; Young et al., 1963; Purser, 1965; Vakil et al., 1968; Turner, 1969; Shelton and Menzies, 1968, 1970; Eikje, 1975). Purser (1965) noted that most reported heritability values are based on single lambings and range from 0.0 to 0.2; the few estimates based on three or more lambings vary from 0.2 to 0.3. Since ewes are commonly kept in a flock for several years and have a number of opportunities to lamb, the higher heritability estimates for litter size may be more realistic (Purser, 1965; Shelton and Menzies, 1968). THe practice of retaining ewes to older ages does however delay selection. Turner (1969) noted that combining yearling lambing records with records from older ewes in data used to estimate heritabilities resulted in significantly lower heritability values.

Although both heritability and repeatability estimates for prolificacy tend to be low, they are still usually higher than corresponding values for other reproductive traits in annual programs. Purser (1965) found that heritability estimates for ewe barrenness were negligible; those for lambs weaned per ewe joined were little higher. Turner (1966, 1969) and Elliott et al. (1979), noting the same trend, suggested that it would be more profitable to select for the number of lambs born or for multiple births

rather than against the failure to lamb.

Under continuous lambing, Iniguez et al. (1986) estimated the heritability of conception rate as .30. Gabina (1989b), however, observed no genetic variation in fertility or age at first lambing in ewes managed in a three times in 2 yr lambing system. When 2 or 3 and greater lambing records per ewe were used, heritability of litter size was .17 and .28, respectively (Gabina, 1989b).

Theory of All-Or-None Traits

Although phenotypes for fertility at seasonal and nonseasonal exposures vary in a discontinuous fashion (a ewe either conceives or fails to conceive), the trait is undoubtedly inherited in manner analogous to continuous traits. The binomial, all-or-none expression of seasonality, however, complicates procedures for evaluating genetic variability and differences among individuals for the trait. Procedures for estimating genetic and phenotypic parameters and breeding values for continuous traits are less adequate for binomial data. Methods for evaluating fine demarcations in genotypes among families and individuals are necessary to enhance selection response.

Genetic theory. Historically, regression and analysis of variance procedures have been used to analyze all-or-none traits. Falconer (1965, 1967) suggested methods for

converting information expressed as incidence or percent expression into regression estimates among relatives. Lush et al. (1948), Robertson and Lerner (1949) and Dempster and Lerner (1950) applied analysis of variance procedures for continuous data to binomial data in which mutually exclusive, alternative phenotypes were assigned metric measures. They further suggested methods of transforming binomial estimates of correlation and heritability to an approximately normal scale.

Despite differences in statistical methodologies, similar theories of the inheritance of all-or-none traits appear in the early literature. Although all-or-none traits are dichotomous in their expression, it is assumed that a continuous underlying variate defines phenotypic expression. This underlying variate has been termed the "liability," emphasizing that it represents all innate and external circumstances which affect manifestation of the trait (Dempster and Lerner, 1950; Falconer, 1965). The correlation of observed incidence with liability is based on the idea of a "threshold." The threshold represents a fixed value along the liability scale. All individuals whose liability exceeds this threshold exhibit the trait while those below the threshold do not (Falconer, 1965).

Variation in liability is assumed to follow an approximately normal distribution. Consequently, the standard deviation can be used as a unit of measure of

liability (Dempster and Lerner, 1950; Falconer, 1965; Van Vleck, 1972). The assumption of a normally distributed liability implies that the genetic component of the trait is either multifactorial, or, if there are few genes, their effect is assumed to be small relative to environmental variation (Falconer, 1965).

Regression. Falconer (1965, 1967) referred to the alternative phenotypic expressions of dichotomous traits as either "normal" or "affected," terminology consistent with his investigations of human disease. Groups of individuals, for example families or the entire population, can have different percentages or incidences of affected individuals. Due to the dependence of the mean and variance with percentage data, Falconer (1965) suggested that incidence should be converted to mean liability. Mean liability is related to the incidence by the normal deviate, x, which is the deviation of the threshold from the mean in standard deviation units of liability.

Falconer's (1965) methodologies can best be explained by example. Suppose the upper distribution in figure 1 represents a parental generation from which affected individuals are selected as parents. The lower distribution represents the liability of offspring of these affected parents. A fixed threshold is shown representing the demarcation between phenotypic classes. A higher incidence (20 vs 5%) and thus mean in the offspring relative to the

parental generation is shown.

To conduct genetic analyses, the difference in the mean liabilities between the two generations and the mean liability of affected individuals in the parental generation is required (Falconer, 1965). For simplicity, the variance of liability of the two generations will be assumed to be equal. Falconer (1967) proposed a scaling procedure to account for differences in variance between the two distributions. The standard deviation of liability is used as the common unit of measure, marked off from the threshold value of zero. For the example incidence, mean liabilities of -1.6 σ and -.8 σ for the parental and offspring distributions are observed. Evaluation of mean liabilities is made by reference to tables of the normal distribution with incidence p and normal deviate x. The difference between the mean liability of the offspring and parental generation represents the response to selection R. For illustrative purposes, it is assumed that the mean liability in the parental generation adequately represents the mean liability in the population contemporary to the offspring generation.

The mean liability of affected individuals in the parental generation is by definition the standardized selection differential S. This liability can also be evaluated by reference to normal tables where S equals the quotient of z, the height of the ordinate at the threshold,

and p, the population incidence. In the cited example, the ratio of R and S is the regression of offspring on the parental mean which provides an estimate of the heritability of liability.

Although useful for illustrative purposes, many of the previously stated assumptions reduce the general utility of these procedures. Falconer (1965) details methodologies for more complex situations involving various sorts of relationships and the use of control populations. Use of a population contemporary to the progeny (or other relations), a control, is necessary for estimating response when variances in the parental and offspring distributions differ. Thompson et al. (1985), as an extension to Falconer's work, proposed mixed model procedures for estimation of heritability by parent-offspring regression when incidence and mean liabilities vary between levels of fixed effects. With these procedures, data on affected and normal parents and their offspring must be available.

Analysis of variance. To apply analysis of variance procedures to incidence data, Lush et al. (1948), Robertson and Lerner (1949), Dempster and Lerner (1950) and Elston et al. (1977) suggest assigning arbitrary values of 1 and 0 to each individual that expresses or fails to express the trait, respectively. These alternative phenotypic measures can be considered crude gradations along some continuum. Variance components can then be calculated in a fashion

consistent with that used for metric traits. This mode of measurement has been referred to as the p scale by Dempster and Lerner (1950).

Use of the p scale may, however, introduce inaccuracies in evaluation of all-or-none traits. The crude gradations of the p scale introduces considerable measurement error when components of variance are estimated (Dempster and Lerner, 1950). Such error would appear as environmental variation and would be dependent on the incidence of the trait. At an incidence around .5, environmental variance would be minimal; with lower or higher incidences, the variance would increase (Falconer, 1981). The categorical nature of measures on the p scale may also obscure finer degrees of variation and thus detection of genetic differences between individuals and families (Dempster and Lerner, 1950).

The probit transformation has been proposed as a method to adjust values on the p scale to a frequency- or incidence- independent scale (Lush et al, 1948; Robertson and Lerner, 1949; Elston et al., 1977). The basic assumption of this transformation is that liability is a continuous and normally distributed variable with a fixed threshold dividing the population into two fractions. The probit value locates the population along the underlying liability scale rather than along the incidence scale (Lush et al., 1948). Heritabilities and intra-class correlation

based on percentages can then be expressed in terms of the more accurate liability scale. The transformation is made by multiplying p scale estimates by:

$$\frac{p\ (1 - p)}{z^2} \quad,$$

where p and z retain their previous definitions (Robertson and Lerner, 1949). The utility of the probit transformation is in allowing equitable comparison among estimates based on data with different incidence. The use of such values to estimate expected rates of gain or to devise indexes is less clear (Dempster and Lerner, 1950).

It is important to note that the work of Lush et al. (1948), Robertson and Lerner (1949) and Dempster and Lerner (1950) was based on viability in poultry. Several years of data on mortality during the first laying year were used. Sire and dam families were large. Variances were estimated on a within-year basis and were often pooled across years. Analyses based on incidence are likely less useful in livestock data where populations are comparatively small and several fixed effects are often present.

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Figure 1. Illustrations of two populations or groups with different mean liabilities. The liability is normally distributed and groups are compared by reference to a fixed threshold. The stippled portions are the affected individuals with the incidences shown (Falconer, 1965).
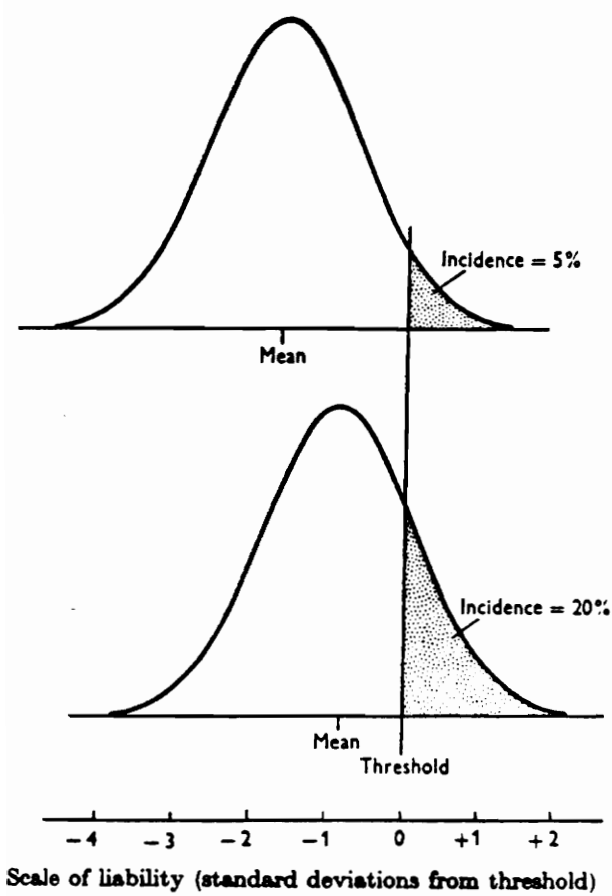
Incidence = 5%

Mean

Incidence = 20%

Mean

Threshold

−4 −3 −2 −1 0 +1 +2

Scale of liability (standard deviations from threshold)

Reproductive Performance of Dorset Ewes in the

STAR Accelerated Lambing System. I. Ewe Fertility

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ABSTRACT

Ewe fertility was evaluated in the STAR accelerated lambing system. Fertility was defined as 1 or 0 depending upon whether a ewe lambed or failed to lamb, respectively, from a given exposure. The STAR program consists of five 30-d concurrent breeding and lambing periods per year beginning on January 1 (S1), March 15 (S2), May 27 (S3), August 8 (S4) and October 20 (S5). Optimally, a ewe could

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lamb every 7.2 mo beginning at 1 yr of age. Records on 1,084 Dorset ewes over 7 yr beginning in S1, 1982 were used. Fertility differed (P < .001) among exposures in S1 (.49), S2 (.28), S3 (.15), S4 (.46) and S5 (.69). In favorable seasons (S1, S4, S5), fertility was .37 ± .02 higher then in unfavorable seasons (S2, S3). An annual periodicity for fertility was observed (R^2 = .79). Linear and quadratic effects of ewe age on fertility were found (P < .001) for ewes under 4 yr of age; no ewe age effect was observed at older ages (P > .50). Regressions of fertility on ewe age differed (P < .05) among seasons. Fertility was reduced (P < .001) at exposures shortly after lambing, but the effect became smaller as the number of seasons since last lambing increased. The number of lambs born and nursed by a ewe at her preceding lambing had little effect on fertility, even at the first postweaning exposure (P > .10). A transition matrix of expected pregnancy rates by season, lambing number and number of seasons since last lambing was constructed. Transition probabilities across sequential exposures differed with the season of lambing (P < .05) and with lambing number (P < .001).
(Key Words: Sheep, Dorset, Accelerated Lambing, Fertility)

Introduction

In many management systems, efficiency of lamb

production could be improved by increasing lambing frequency. To increase the frequency of lambing, some proportion of the ewes in a flock must exhibit estrous during the typically anestrous period between March and June. Although cyclicity during this period can be induced by light and (or) hormone treatment, these practices require confinement of animals and greater inputs of labor, housing and energy. Extension of the fertile period by altering gene frequencies within sheep populations would provide permanent, cumulative changes in breeding patterns. However, the binomial, all-or-none expression of fertility (i.e., a ewe either conceives or fails to conceive) complicates evaluation of genetic differences among individuals in fertility. Methods for more accurate estimation of breeding values for fertility are thus required to enhance selection response.

Many multiple-season lambing programs have been proposed, including continuous lambing, twice-yearly lambing or lambing three times in 2 yr (Walton and Robertson, 1974; Notter and Copenhaver, 1980; Fogarty et al., 1984; Gabina, 1989). One objective of this study was to describe reproductive performance in the STAR accelerated lambing system (Hogue, 1986). In order to evaluate genetic differences among animals in ability to perform in STAR, effects of environmental factors must first be quantified and removed. These environmental factors potentially

include effects of ewe age, season of birth, number of seasons between lambing and exposure, and number of lambs produced and nursed at the previous lambing. Techniques for expressing fertility on a more continuous scale were also investigated.

Materials and Methods

Management.

The STAR accelerated lambing system was developed at Cornell University in 1982 and involves five lambings per year. The calendar year is divided into five 73-d seasons (figure 2) which begin on January 1 (S1), March 15 (S2), May 27 (S3), August 8 (S4) and October 20 (S5), respectively. During the first 30 d of each season, ewes are either lambing or are exposed to rams. Ewes lactate for 36 to 66 d. Lambs are weaned 7 d before introduction of a ram at the start of the next season. All nonlactating ewes are exposed to a ram in each season.

The shortest mean interval between lambings is 219 d (7.2 mo). Failing this, ewes can either lamb after 292 d (9.6 mo) or on an annual (or longer) lambing cycle. A ewe could lamb a maximum of five times in 3 yr, which would require that she conceive in each of the five seasons. Ewe lambs are exposed to rams at 7 to 8 mo of age and can lamb first at 1 yr of age.

The Dorset flock at Cornell University was managed under the STAR system with three breeding groups: A, B and C. Rams born in flocks A, B and C generally served as sires for flocks B, C and A, respectively. Purchased rams were also occasionally used. All matings were in single sire-pens. Ewe lambs were routinely exposed to Finnish Landrace rams and multiparous ewes with long lambing intervals were occasionally exposed to Suffolk rams. Typically, breedings in S1, S4 and S5 fall within the normal breeding season of the sheep and these seasons will henceforth be referred to as favorable seasons. S2 and S3 exposures fall outside the normal breeding season and will be referred to as unfavorable seasons (Dufour, 1974; Fogarty et al., 1984).

Retained and purchased Dorset rams were selected from twin and triplet litters and(or) from ewes with a history of fall or accelerated lambings. Only one ram from outside the flock was used after the S1, 1983 exposure. All rams selected after 1984 had dams with at least five consecutive 7.2 mo lambing intervals. These dams are henceforth referred to as all-STAR ewes. Among the 57 sires of ewes represented in the data, 14 were purchased from ten outside breeders, 17 were born in an accelerated lambing system preceding STAR, and 26 were born in STAR. STAR-born rams included four pairs of maternal half-sibs and three pairs of full-sibs, including one pair of litter mates. Sixteen of the 26 rams had all-STAR dams. Thirty-six rams were used as

service sires within the STAR system. Minimal selection among ewes was practiced. Ewes that lambed following long intervals (often in excess of 2 yr) or that tested positive for ovine parainfluenza pneumonia (OPP) were generally culled.

Ram to ewe ratios varied widely by breeding group, year and season, ranging from 5 to 198 ewes per ram. Depressed fertility in some year-season combinations may result from the large numbers of ewes exposed to an individual ram and from poor fertility in some rams, especially during unfavorable seasons (S2 and S3). For instance, among 181 ewes exposed in breeding group B in S3, 1987, none lambed.

Dry and gestating ewes were maintained on improved mixed grass-clover pasture from mid-May to early November. During winter, ewes received about 1.8 kg of hay/d. Ewes were confined for about 70 d during late gestation and lactation and fed approximately 2.3 kg of hay 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.

Data.

Lambing records on 1,084 Dorset ewes from S1 of 1982 through S4 of 1988 were used. Of these ewes, 742 were born in the STAR system and contribute records starting in S1 of 1983. An additional 342 ewes were born in the Cornell

alternate month accelerated lambing (CAMAL) system. In the CAMAL system, breeding and lambing occurred in alternate months, allowing for average lambing intervals of 6, 8, 10 and 12 mo (Hogue et al., 1980; Iniguez et al., 1986). Complications in management of the CAMAL system led to development of the STAR system (Hogue, 1986).

Records on 7,269 exposures which resulted in 3,048 lambings and production of 4,642 lambs were available. Traits measured included lamb birth type and date, sex, rearing type and weaning date and weight. Lambs born in large litters or whose dams tested positive for OPP were either fostered or raised artificially. Only lambs that nursed their dams to weaning were considered reared. Although specific exposure lists were unavailable, exposure data were generated based on lambing, culling and death records, and on a flock inventory conducted in S4, 1988. Numbers of ewes present, exposed and lambing and numbers of lambs born are shown by year and season in table 1.

Four reproductive traits were defined. Prolificacy and rearing type were scored as 1, 2 or 3 for single, twin or triplet birth and rearing. Fertility was coded as 1 for ewes that lambed and 0 for ewes that failed to lamb from a given exposure. Lamb survival was coded as 1 and 0 for lambs that were or were not present at weaning.

Environmental factors that were considered included ewe age, season of birth, prolificacy and nursing status at the

ewe's previous lambing, and interval between lambing and exposure. Ewe age was expressed in seasons (S) since birth, with five seasons per year corresponding to the five STAR seasons. Thus, a 4-yr-old ewe would be designated as 20 S. Birth dates for ewes born in the CAMAL system were used to categorize CAMAL ewes into birth seasons analogous to those used in STAR. Lambings were also categorized by number as first, second, third or fourth and greater. Early lambing records on CAMAL ewes were not included in the data, so CAMAL ewes that first lambed at between 8 and 10 S, 11 and 13 S and at 14 S or longer were given lambing numbers of 2, 3, and 4, respectively. Records on CAMAL ewes that lambed at less than 8 S were removed.

Ewes were categorized with regard to prolificacy and nursing status (PNS) at a prior lambing as those that produced: single or multiple lambs that did not survive (1-0 and 2-0, respectively); a single and nursed one or two lambs (1-1); or twins or triplets and nursed one (2-1) or multiple (2-2) lambs. The exposure interval defined the number of seasons post-lambing before a ewe became pregnant. Ewes that lambed from their first exposure season following a previous lambing were assigned an interval of 1. A lambing interval of up to 5 was defined in this manner; longer intervals received a common code of 6.

Inbreeding levels within the flock were evaluated by procedures proposed by Quaas (1976) under the assumption

that CAMAL and purchased animals were unrelated. Since only lambings within the STAR system were considered, some relationships among CAMAL ewes were lacking. The average level of inbreeding calculated for the flock thus is likely a slight underestimate (Iniguez et al., 1986). Only records on STAR ewes were used to evaluate inbreeding effects.

Statistical Procedures.

Seasonal periodicities.

Since an annual pattern of high and low fertility during unfavorable and favorable season exposures, respectively, was expected, nonlinear procedures were used to model predictable seasonal changes in fertility. The regression of mean fertility on consecutively numbered year-season combinations was fit to adjust for linear trends in fertility. Residuals from this analysis were then used as the response in a periodic model similar to that used by Stroup et al. (1987):

$$Y_t = \alpha_1 \sin(2\pi t/A) + \alpha_2 \cos(2\pi t/A)$$

where Y_t was the residual fertility for the tth year-season combination, 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 nonlinear regression

procedure of SAS (1985). In addition, A was also fixed at 5 S to produce a yearly periodicity. Reduced models including only the sine or cosine function were also fit to test significance of α_1 and α_2.

Ewe age. Effects of ewe age on fertility were considered using model 1:

$$Y_{ijklm} = \mu_Y + B_i + R_j + I_k + (BR)_{ij} + (BI)_{ik} + (RI)_{jk} +$$

$$(BRI)_{ijk} + S_1 + \beta_1(X_{ijklm} - \mu_X) + \beta_2(X_{ijklm} - \mu_X)^2 +$$

$$[\beta_{1i}(X_{ijklm} - \mu_X)B_i] + [\beta_{2i}(X_{ijklm} - \mu_X)^2 B_i] +$$

$$[\beta_{11}(X_{ijklm} - \mu_X)S_1] + [\beta_{21}(X_{ijklm} - \mu_X)^2 S_1] +$$

$$\epsilon_{ijklm},$$

where Y_{ijklm} was the fertility of kth ewe (I) born in the jth year (R) and the ith season (B) and lambed in the 1th season (S). μ_Y was a constant common to all observations, β_1 and β_2 were linear and quadratic regression coefficients, respectively, of fertility on ewe age in seasons, X_{ijklm} was ewe age at each exposure, and μ_X was the mean ewe age. β_{1i} and β_{2i} were linear and quadratic regression coefficients, respectively, of age within ewe birth year, β_{11} and β_{21} were linear and quadratic regression coefficients, respectively, of age within lambing season, and ϵ_{ijklm} was a random error term associated with each record. To prevent confounding of

age effects with genetic and permanent environmental effects among ewes age, effects were estimated after absorption of ewe effects. Year of lambing could not be explicitly considered in the model since it was completely defined by the combined effects of ewe, season of lambing and age.

Effects of system of origin of the ewe (STAR vs CAMAL) were added to model 1, with effects of ewe birth season and year and of ewe nested within system. This model (model 2) also included The interaction of lambing season with ewe birth system.

Interval. Effects of exposure interval on fertility were subsequently added to models 1 and 2. Addition of this effect precluded use of records preceding the first pregnancy and reduced the data set to 2,596 and 2,068 exposures for STAR and CAMAL ewes, respectively.

Pregnancy and nursing status. Effects of PNS were anticipated to be important only in exposures that immediately followed weaning. Thus, data including only interval 1, STAR-born ewes were used to evaluate effects of PNS. A total of 1,175 records were available and were analyzed by adding effects of PNS to model 1.

Inbreeding. Inbreeding coefficients ranged from 0 to .25 for STAR ewes. All ewes with inbreeding levels exceeding 19% were daughters of a single purchased ram. Since the ancestry of this ram was unknown and the fertility of these ewes differed from the remainder of the flock,

their records were excluded from analysis. Records on two ewes with unknown sires were also removed, leaving 3,153 records, which were analyzed to determine inbreeding effects using model 3:

$$Y_{ijklmn} = \mu_Y + B_i + R_j + M_k + (BR)_{ij} + (BM)_{ik} + (RM)_{jk} +$$
$$(BRM)_{ijk} + S_l + C_m + (SC)_{lm} + \tau \, (Z_{ijklmn} - \mu_Z) +$$
$$\epsilon_{ijklmn},$$

where Y_{ijklmn} was the fertility of a daughter of the kth sire (M) born in the jth year (R) and i^{th} season (B), and lambing in the lth season (S) and m^{th} year (C). τ was the regression of fertility on inbreeding level of the ewe, Z_{ijklmn} was the inbreeding coefficient for the ewe, and μ_Z was the mean level of inbreeding. An additional model used 1,745 records made after the first lambing to consider effects of exposure interval.

Transition probabilities. Once determining which environmental factors affected fertility, a procedure for tracing a ewe's lifetime reproductive history that characterized these effects was deemed necessary. Within STAR, many production pathways are possible. By 2 yr of age, a ewe could have followed any of 27 different sequences of exposures and lambings, with the number of possible branchings continuing to increase exponentially as she aged.

Rather than attempting to differentiate each unique reproductive history, a methodology for relating an expected probability of conception to each season of exposure and ewe age was developed.

A transition matrix based on points of intersection among pathways was designed. Rows of the matrix were combinations of previous lambing season and lambing number, with ewe lambs initially placed in the matrix based upon their birth season. Columns of the matrix represented the number of exposures since lambing (or first exposure for ewe lambs). Each cell in the matrix represented a transition probability (TP) which was the estimated probability that a ewe would lamb from the exposure. Successes define a new previous season of lambing and lambing number and transition to a different row in the matrix. Ewes that do not conceive from a given exposure pass to the next column within a row of the matrix.

Transition probabilities were estimated separately for STAR and CAMAL ewes and for combined data. Two sets of probabilities were calculated. Simple proportions (SP) were the ratio of numbers of ewes succeeding to number of ewes entering an interval. For each year where 5 or more ewes were present at interval 1, the proportion of ewes succeeding at each interval was computed. The mean of these proportions were termed least-squares proportions (LSP). Ewes that reached interval 6 without becoming pregnant were

considered chronically barren and assigned TP's of zero. To detect whether SP and LSP estimates differed, 95% confidence limits corrected for continuity (Snedecor and Cochran, 1980) were calculated for each SP estimate; overlap of LSP and SP estimates was taken to indicate that there was little difference between the estimates.

The propriety of combining STAR and CAMAL records to estimate TP was evaluated by determining whether percentages of ewes becoming pregnant were homogeneous between systems for each previous lambing season, lambing number and exposure interval. Tests were based on chi-square procedures for analysis of two by two contingency tables. Following correction for continuity, a Z statistic and its associated P-value were derived from the square root of the chi-square statistic (Snedecor and Cochran, 1980).

Effects of previous lambing season and ewe age on the distribution of pregnancies across sequential exposures was determined using the Lee-Desu test statistic (Lee and Desu, 1972; SPSS, 1985). This nonparametric procedure tests whether subgroups (i.e., ewes differing in previous lambing season or lambing number) come from the same distribution based on a score for mean interval to pregnancy. Thus differences in time (number of intervals) to pregnancy are quantified. Pregnancy patterns among ewes differing in lambing number were compared within each season of previous lambing and vice versa. Since ewes left the flock at

various times and data collection ended at S4, 1988, data on some ewes ended before they became pregnant. Final records on such ewes were considered censored data in calculations of the Lee-Desu statistic (Lee and Desu, 1975; SPSS, 1985).

Results and Discussion

Flock performance.

Simple means and SE for fertility, prolificacy and lamb survival and for age and weight at weaning are shown by exposure season and system of ewe origin (STAR or CAMAL) in table 2. Average fertility was higher at favorable (.54) than at unfavorable (.21) exposure seasons although prolificacy and lamb survival were similar. Prolificacy was higher for ewes bred in S3 (June) than for ewes bred in S1 (January), possibly due to a flushing effect in ewes bred on spring forage. Heavier weaning weights among lambs from S5 and S1 matings correspond with their older ages and reflect earlier lambing dates in ewes exposed in favorable seasons.

Fertility among STAR and CAMAL ewes was similar. CAMAL ewes had .07 higher average pregnancy rates from S3 and S4 exposures and tended to be more prolific than STAR ewes. These differences in performance probably reflect age differences. CAMAL ewes were approximately 10 S (2 yr) older then STAR ewes at all seasons. The mean age at lambing for STAR and CAMAL ewes was 11.3 ± .1 (over 2 yr)

and 21.4 ± .3 S (over 4 yr), respectively, with maximum ages of 33 and 63 S, respectively. Over 90% of records on STAR-born ewes represented animals under 20 S. Among CAMAL-born ewes, ewes under 30 S defined a similar percentage of data.

Mean inbreeding coefficients for STAR and CAMAL ewes were .026 and .009, respectively. Lower inbreeding levels for CAMAL ewes partly reflect missing ancestry information in older animals. The average inbreeding coefficient of 175 CAMAL ewes born after 1980 was .018. Mean inbreeding increased with time from 1% in 1982 to 2.5% in 1988. Inbreeding coefficients were less then .0625 for 98% of the ewes; 59% were noninbred. Intentional linebreeding of one purchased ram through sire-daughter matings produced inbreeding levels of 25% in 20 daughters and 1 son that was retained as a sire.

Among all ewes, 42 or 3.9% were all-STARS. Ten ewes lambed at seven consecutive minimum intervals and, on average, produced 10.5 ± .7 lambs (2.5 lambs/yr) and weaned 137.9 ± 1.8 kg of lamb within 50.4 mo. (32.8 kg/yr). The average ewe lambed .84 times/yr, giving birth to and rearing 1.52 and 1.25 lambs, respectively, and weaned 20.4 kg of lamb/yr.

Fertility

Seasonal effects and periodicity. Effects of lambing season on fertility were similar for STAR and CAMAL ewes.

Fertility during favorable season exposures was .37 ± .02 greater than that at unfavorable seasons (P < .001). Relative to May exposure (S5 lambing), fertility in October was .57 ± .02 higher; January and August exposures had a smaller advantage of .41 ± .02 and .31 ± .01, respectively. Fertility in March was slightly superior (.12 ± .02) to that in May. Fertility in CAMAL ewes tended to be less variable across seasons than in STAR ewes. However, in relation to May exposures, CAMAL ewes were less fertile than STAR ewes in March exposures (.06 ± .03 vs .16 ± .02).

No linear trend (P > .50) over time was observed for fertility. Much of the variation in fertility was defined by the periodic model (R^2 = .79), suggesting that predictable seasonal variation in fertility was present. A periodicity of 5.08 S was obtained and did not differ (P < .10) from an annual (5 S) periodicity. For A = 5 S, parameter estimates (P < .01) for α_1 and α_2 were .117 and −.221, respectively.

Predicted and observed values for fertility aligned closely and are shown relative to the observed mean fertility (.421) in figure 3. Low fertilities at S2 and S3 exposures (S4 and S5 lambings) tended to be underestimated by the model. The markedly low fertility (.058) at the S5, 1987 lambing reflects infertility of one ram that was used heavily. With the exception of lambings in S5 from S3 (March) exposures, extremes in fertility and prolificacy

tended to correspond (Lewis et al., 1990a).

Environmental factors. Analyses of variance for models 1 and 2 are shown in table 3. In all models, lambing season, exposure interval, linear and quadratic ewe age effects and the interaction of ewe age with lambing season were significant. In model 2, interaction between lambing season and ewe birth system was also present (P < .001).

In models excluding exposure interval, ewe age interacted with birth season (P < .05). Inclusion of exposure interval, however, removed this interaction effect in the data used to evaluate interval effects. This result is at least partly due to the removal of first lambing records since first lambing records would likely be most sensitive to birth season effects. These results thus suggest a complex relationship among lambing and birth season, exposure interval and ewe age.

Maximum fertility among STAR and CAMAL ewes considered together and among CAMAL ewes alone was reached at approximately 5 yr (26 S) and decreased thereafter. For STAR ewes, an earlier maximum was observed (16 S). Since few CAMAL ewes were older then 30 S and few STAR ewes were above 20 S, it appears that ewe age at maximum fertility occurred near the maximum ewe age represented in the data. Such a pattern would be expected if linear and quadratic polynomials were being applied to a relationship that was actually asymptotic, so subsets the data were subsequently

created to investigate this possibility. When records among ewes below and above 20 S were separately evaluated with models 1 and 2, no age effects (P > .50) were observed among older ewes. For STAR and combined data, significant linear (.0453 and .0310, respectively) and quadratic (-.0015 and -.0007, respectively) regression coefficients were obtained for ewes under 20 S with maximum fertility at 15 and 22 S, respectively. A strictly linear age effect was seen in CAMAL ewes (regression coefficient of .0163; P < .001). These results suggest a curvilinear relationship between age and fertility which asymptotes to a stable mean fertility at about 4 yr of age.

Constants for exposure interval were expressed as deviations from the 6 and upward category and were similar for both groups of ewes. Lower fertility at shorter exposure intervals was observed. For combined data (model 2 with inclusion of interval effects), constant estimates were -.274 ± .040, -.168 ± .040, -.099 ± .041, -.069 ± .045 and -.018 ± .051 for intervals 1, 2, 3, 4 and 5, respectively. Thus, fertility at exposures soon after weaning is lower.

For individual lambing seasons, S1 and S4 (corresponding to exposures in S4 and S2, respectively) appeared most sensitive to environmental effects. Although exposure interval explained variation in all seasons (P < .01), ewe age effects (linear: P < .01; quadratic: P < .05)

and their interaction with birth season (P < .1) were only important at exposures in S2 and S4. Heightened environmental sensitivity in these seasons may reflect their transitional role between favorable and unfavorable exposure periods.

Pregnancy and nursing status (PNS) effects at a ewe's previous lambing within interval 1 for STAR-born ewes were small (P > .10). Constant estimates relative to the 2-2 category were -.122 ± .079 for 1-0, -.051 ± .041 for 1-1, -.161 ± .106 for 2-0, and .064 ± .061 for 2-1. At first post-lambing exposure, ewes that lambed but did not wean a lamb tended to have lower fertility than ewes that raised a lamb. Thus adjustment for PNS would elevate the fertility of ewes that did not wean a lamb. Some ewes that do not wean lambs may exhibit some form of unsoundness, and these unsoundnesses may compromise subsequent fertility. In any case, PNS adjustment to fertility appears inappropriate because it would give credit to ewes that fail to wean at least one lamb.

Inbreeding. A decrease in fertility with increasing level of inbreeding was observed (τ = -.711 ± .322; P < .05). Within the practical range of inbreeding present in the flock, a reduction in fertility of .081 between ewes with inbreeding coefficients of 0 and .125 would be expected. For individual seasons, inbreeding was important only at S2 exposures (P < .05), where an increase of .01 in

inbreeding corresponded to a .019 reduction in fertility. When exposure interval was considered, no inbreeding depression was found across or within specific seasons (P > .20). Thus for these data, no clear interpretation of inbreeding effects on fertility was evident.

Transition probabilities. Results of least-squares analyses suggested that effects of season of ewe birth and exposure, ewe age, interval since lambing and their interactions all define environmental variation in fertility. As an alternative to defining age in terms of seasons, intersections between production pathways could be more conveniently expressed when age was defined by lambing number. Within a lambing number, age (in seasons) progressed across exposure intervals in a predictable manner. For STAR ewes that first lambed in S1, mean ages at each exposure interval were 9.07 (1), 9.95 (2), 11.01 (3), 11.94 (4), 12.87 (5) and 13.83 (6+) S. This near-unit change in age across intervals was consistent among ewe birth systems, previous lambing seasons and lambing numbers. Thus, although incremental accounting for seasonal age increases was not intrinsic to classification into lambing number, the combination of exposure interval and lambing number closely approximated the ewe age distribution.

Average ages by lambing number for STAR and CAMAL ewes, respectively, were 10.17 and 10.18 S for lambing number 2, 14.22 and 14.23 S for lambing number 3, and 20.65 and 25.87

S for lambing number 4 or later. At first lambing, STAR ewes averaged 6.20 S. Through third lambing, age at each lambing among STAR and CAMAL ewes corresponded closely. The minimum age at each lambing number was 4, 7, 10 and 14 S, although only rarely were ewes bred at 2 S to first lamb at 4 S (5% of ewes).

In estimation of TP, correlations between repeated records on ewes exposed more than once within the same season were not considered. The average number of lambings among ewes within a previous lambing season were 1.51 (S1), 1.28 (S2), 1.15 (S3), 1.13 (S4) and 1.11 (S5). Among the 2,252 lambings contributing to estimation of TP, 78.2% represent ewes that lambed only once within the season; in only 3.7% of the lambings were 3 or more records within a season defined by a single ewe. Bias associated with repeated records on ewes was thus likely to be small.

Overlap in a 95% confidence limit for SP was used to detect differences between transition probability estimates based on SP and LSP. Among 64 and 113 comparisons for CAMAL and STAR records, respectively, 64 (100%) and 105 (92.9%) of the LSP fell within the SP confidence limit. Among STAR records, differences between estimates tended to occur at later intervals where subclass numbers were small. When TP were based on combined STAR and CAMAL records, SP and LSP differed in 6.1% (7 out of 115) of the comparisons. Since use of either estimate appeared justified, TP estimates

based on SP were chosen in order to simplify the nonparametric procedures used later for comparing time to pregnancy across previous lambing seasons and lambing numbers.

Since differences in the effect of certain environmental factors were observed for STAR and CAMAL data, SP for each previous lambing season, lambing number and interval combination were compared across systems. First lambings were necessarily excluded. Intervals in which all or no ewes settled to an exposure were also ignored. Among 55 comparisons, 7 suggested that probability estimates for STAR and CAMAL ewes differed (P < .05). At interval 1, lambing number 3 and 4, and previous lambing season S1, a marked difference (P < .001) between ewes born in the two systems was observed; fertility among STAR ewes was .28 and .20 higher than that for CAMAL ewes. These lambings corresponded with S2 exposures which previously were noted to be less fertile in CAMAL ewes. In all but one instance (season 2, lambing number 4, interval 1; P < .01) other differences occurred at long intervals where sampling errors were large. With the exception of March exposures, these results support combining of STAR and CAMAL data to estimate TP and the use of a single probability to predict fertility records for ewes born in both systems.

Transition probabilities and SE based on joint STAR and CAMAL data are shown in tables 4 and 5. Separate TP for

STAR and CAMAL ewes at season-interval combinations leading to S2 exposure are given. In certain instances, no records on CAMAL ewes were available at these junctions. All probabilities for first lambings were estimated from STAR data. When studying TP estimates at each exposure interval across previous lambing seasons and lambing numbers, considerable heterogeneity among estimates was evident. For previous lambings in S1 and S2, for instance, low TP at interval 1 (and interval 2 for S1), correspond with exposures at unfavorable seasons. At later intervals, with exposures during favorable seasons, TP increase markedly. For previous lambing seasons leading to early, favorable exposures, TP tend to be high and decrease at later intervals with exposures during unfavorable periods. Generally, with increasing lambing number, TP increased across all intervals.

These suppositions were validated using nonparametric methodologies. Interval to conception differed with previous season of lambing (P < .05) and lambing number (P < .001). In table 6, median intervals, Lee-Desu test statistics and nonparametric multiple comparisons based on mean interval scores are shown for combined STAR and CAMAL data. Median intervals were longer for previous lambing seasons which led to an unfavorable exposure (S2 or S3) at interval 1. This trend is particularly clear in previous lambing season 1 where ewes failing at their interval 1

exposure (S2) would be re-exposed at S3. Median interval length for previous lambing season S3 tended to be longer then for S5, although clear differences were not present (P > .05). This tendency may reflect a transition from unfavorable to favorable breeding seasons among ewes lambing in S3 with their first exposure in August. The interval to fertile exposure decreased as ewes aged (P < .05), with shortest periods between lambings seen for ewes at their fourth or later parturition.

The utility of transition probabilities surpasses simply characterizing seasonal, age and interval effects on fertility. More importantly, these probabilities can be used to express the 0 or 1 measure of fertility on a more continuous scale. Procedures for estimating phenotypic and genetic parameters for continuous traits can then be applied to fertility. Applications of these methodologies are detailed in Lewis et al. (1990b).

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TABLE 1.   NUMBERS OF EWES, EXPOSURES, LAMBINGS AND LAMBS
BORN FOR STAR AND CAMAL EWES BY SEASON AND YEAR OF LAMBING

	Accelerated lambing system in which ewe was born							
	STAR				CAMAL			
	Exposure[a]		Lamb-ings[b]	Lambs[c]	Exposure[a]		Lamb-ings[b]	Lambs[c]
Class	Ewes	Exp			Ewes	Exp		
Season[d]								
1	647	1,234	527	812	338	889	448	699
2	637	1,043	717	1,137	302	578	395	615
3	367	494	253	349	190	292	135	204
4	454	716	210	279	233	494	134	198
5	563	918	113	166	270	611	116	183
Year								
1982					342	951	337	464
1983	110	249	68	77	272	702	314	463
1984	220	554	229	300	213	513	228	372
1985	300	661	295	426	165	359	174	306
1986	400	941	379	570	96	188	104	173
1987	472	1,120	407	650	43	90	43	76
1988	434	880	442	720	27	61	28	45
Total		4,405	1,820	2,743		2,864	1,228	1,899

[a]Number of ewes exposed (ewes) and number of exposures (exp) within a season or year.

[b]Number of lambings.

[c]Number of lambs born.

[d]Season starting dates: 1 - January 1;   2 - March 15;   3 - May 27;   4 - August 8;   5 - October 20.

TABLE 2. MEAN ± SE FOR PRODUCTION TRAITS BY SEASON OF EXPOSURE
AND ACCELERATED LAMBING SYSTEM IN WHICH THE EWE WAS BORN

			Production traits			
	Ewe					Lamb weaning
S^a	birth system	Fertility	Prolificacy	Lamb survival	Age (d)	Weight (kg)
1	STAR	.51 ± .02	1.38 ± .03	.85 ± .02	63.0 ± .5	17.41 ± .30
	CAMAL	.46 ± .03	1.51 ± .05	.73 ± .03	57.0 ± .6	16.20 ± .37
	Both	.49 ± .02	1.42 ± .03	.80 ± .02	60.9 ± .4	17.01 ± .23
2	STAR	.29 ± .02	1.33 ± .03	.86 ± .02	52.0 ± .7	14.56 ± .31
	CAMAL	.27 ± .02	1.48 ± .04	.86 ± .02	53.6 ± .6	15.30 ± .32
	Both	.28 ± .01	1.39 ± .03	.87 ± .02	52.6 ± .5	14.87 ± .23
3	STAR	.12 ± .01	1.47 ± .05	.70 ± .04	52.4 ± .8	14.97 ± .41
	CAMAL	.19 ± .02	1.58 ± .05	.77 ± .03	52.3 ± .7	15.56 ± .40
	Both	.15 ± .01	1.52 ± .04	.74 ± .02	52.4 ± .5	15.31 ± .29
4	STAR	.43 ± .01	1.54 ± .02	.83 ± .01	54.2 ± .3	15.90 ± .18
	CAMAL	.50 ± .02	1.56 ± .03	.81 ± .01	47.9 ± .4	14.50 ± .18
	Both	.46 ± .01	1.55 ± .02	.82 ± .01	51.3 ± .3	15.25 ± .13
5	STAR	.69 ± .01	1.59 ± .02	.84 ± .01	58.4 ± .3	17.06 ± .17
	CAMAL	.68 ± .02	1.56 ± .03	.80 ± .02	55.7 ± .4	15.93 ± .16
	Both	.69 ± .01	1.58 ± .02	.82 ± .01	57.5 ± .2	16.66 ± .13

[a]Season starting dates: 1 - January 1; 2 - March 15; 3 - May 27; 4 - August 8; 5 - October 20.

TABLE 3. MEAN SQUARES FROM THE ANALYSIS OF VARIANCE OF
FERTILITY AFTER ABSORPTION OF EFFECTS OF EWE BIRTH
SYSTEM (MODEL 2 ONLY), YEAR AND SEASON AND OF EWE

| | | Model 1 | | | | Model 2 | |
| | | STAR | | CAMAL | | | |
Source[a]	df[b]	W/O[c]	With[c]	W/O[c]	With[c]	W/O[c]	With[c]
S	4	5.43***	.83***	3.70***	1.82***	9.63***	2.45***
Int	5		4.14***		.88***		4.15***
Age							
Lin	1	7.31***	.90*	1.94**	.79*	8.43***	2.32***
Quad	1	6.06***	1.64**	1.66**	1.32**	7.61***	3.37***
Age X S							
Lin	4	2.05***	.77**	.82**	.73**	2.40***	1.20***
Quad	4	1.49***	.60*	.55*	.57*	1.30***	.70**
Age X B							
Lin	4(9)	.52*	.22	.55*	.35	.45*	.29
Quad	4(9)	.51*	.24	.37	.33	.62***	.32✝
S X Sys	4					1.93***	1.97***
Residual[d]		.19	.18	.20	.18	.19	.18
R^2		.34	.40	.30	.36	.32	.37

[a]S is lambing season, int is exposure interval, age is the age of the ewe in seasons, B is birth season and sys is the accelerated lambing system in which the ewe was born.

[b]Degrees of freedom shown in parentheses are for model 2, in which birth season was nested within ewe birth season.

[c]Refers to model without (W/O) and with interval.

[d]Residual degrees of freedom across columns were 3,641, 2,058, 2,500, 1,774, 6,149 and 3,845, respectively.

✝P < .10.

*P < .05.

**P < .01.

***P < .001.

TABLE 4. TRANSITION PROBABILITIES BY PREVIOUS
SEASON OF LAMBING, LAMBING NUMBER AND EXPOSURE INTERVAL[a]

Prev lambing season	Lambing number[c]	Exposure interval[b]				
		1	2	3	4	5
1	1	.131	.097	.262	.629	.696
	2	.228/.071	.179	.544	.575	.412
	3	.366/.078	.225	.570	.432	.381
	4+	.573/.368	.254	.579	.707	.467
2	1	.117	.397	.707	.417	.429
	2	.131	.494	.672	.722	.600/.000
	3	.072	.507	.711	.364	1.000/.250
	4+	.144	.599	.774	.238	.125/.333
3	1	.357	.716	.385	.063	.133
	2	.352	.544	.192	.375/.000	.000
	3	.407	.625	.333	.750/	.000
	4+	.599	.643	.150	.556/.333	.000
4	1	.695	.500	.000	.115	.130
	2	.700	.667	.000/	.000	.500
	3	.825	.500	.000/	.000	1.000
	4+	.823	.424	.500/.222	.000	.600
5	1	.573	.031	.035	.393	.765
	2	.571	.222/	.286	.400	.667
	3	.645	.444/.333	.400	.500	1.000
	4+	.727	.700/.400	.231	.333	.333

[a]Transition probabilities are the probabilities that a ewe exposed in an interval will lamb. For intervals leading to exposures in S2, separate probabilities for STAR and CAMAL ewes are listed consecutively. Blanks correspond with the absence of CAMAL ewes.

[b]Interval from previous lambing to given exposure.

[c]Lambing number. Transition probabilities for lambing number 1 were derived from STAR data only.

TABLE 5. BINOMIAL SE FOR TRANSITION PROBABILITIES
BY SEASON OF LAMBING, LAMBING NUMBER AND INTERVAL[a]

Prev lambing season	Lambing number[c]	Exposure interval[b]				
		1	2	3	4	5
1	1	.033	.031	.048	.061	.096
	2	.036/.069	.036	.052	.078	.119
	3	.040/.038	.040	.053	.081	.106
	4+	.049/.029	.031	.041	.060	.129
2	1	.037	.059	.071	.142	.187
	2	.020	.031	.042	.075	.219/.000
	3	.028	.057	.074	.145	.000/.217
	4+	.021	.032	.043	.093	.117/.193
3	1	.028	.033	.068	.043	.062
	2	.051	.066	.077	.121/.000	.000
	3	.095	.121	.193	.217/	.000
	4+	.041	.064	.080	.166/.193	.000
4	1	.033	.065	.000	.063	.070
	2	.103	.193	.000/	.000	.354
	3	.060	.204	.000/	.000	.000
	4+	.027	.086	.204/.139	.000	.155
5	1	.057	.031	.034	.092	.103
	2	.108	.139/	.171	.219	.272
	3	.061	.117/.272	.155	.204	.000
	4+	.041	.145/.110	.117	.157	.193

[a]Transition probabilities are the probabilities that a ewe exposed in an interval will lamb. For intervals leading to exposures in S2, separate probabilities for STAR and CAMAL ewes are listed consecutively. Blanks correspond with the absence of CAMAL ewes.

[b]Interval from previous lambing to given exposure.

[c]Lambing number. Transition probabilities for lambing number 1 were derived from STAR data only.

TABLE 6. MEDIAN INTERVALS, LEE-DESU TEST STATISTICS AND
MULTIPLE COMPARISONS FOR COMBINED STAR AND CAMAL EWES
BY SEASON OF PREVIOUS LAMBING AND LAMBING NUMBER

Prev seas[a]	Lambing number				L-D stat[b]
	1	2	3	4+	
1	$3.72^{c,f}$	$2.91^{d,f}$	$2.62^{d,f}$	$1.94^{e,f}$	72.77***
2	$2.59^{c,g}$	$2.36^{c,g}$	$2.41^{c,f}$	$2.19^{d,g}$	10.45*
3	$1.81^{c,h}$	$1.92^{c,h}$	$1.50^{c,d,g}$	$1.35^{d,h}$	19.36***
4	$1.22^{c,i}$	$1.42^{c,h}$	$1.10^{c,d,h}$	$1.11^{d,i}$	11.73**
5	$1.41^{c,h}$	$1.44^{c,d,h}$	$1.28^{c,d,g,h}$	$1.17^{d,i}$	12.97**
L-D stat[b]	130.22***	22.79***	66.40***	193.67***	

[a]Season of previous lambing. Season starting dates were: 1
- January 1; 2 - March 15; 3 - May 27; 4 - August 8; 5 -
October 20.

[b]Lee-Desu statistics down the column and across the row
refer to comparisons among lambings numbers within a previous
season of lambing and among previous season of lambings within a
lambing number, respectively.

[c,d,e]Within row entries, superscripts that do not have a
common superscript letter indicate mean scores differ (P < .05).

[f,g,h,i]Within column entries, superscripts that do not have
a common superscript letter indicate mean scores differ (P <
.05).

Figure 2. STAR accelerated lambing system

STAR

Accelerated Lambing System
Cornell University November 1983
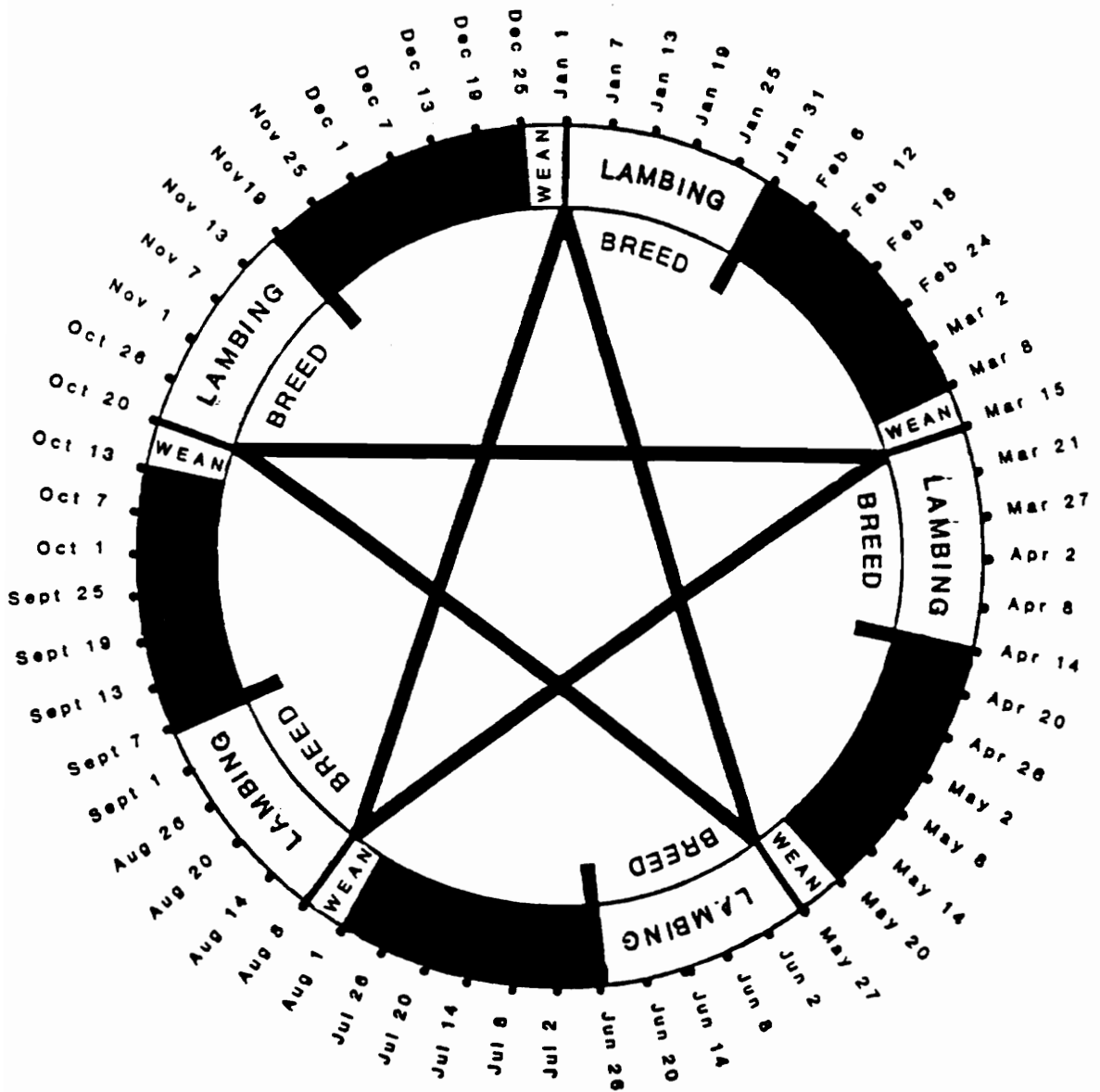
Figure 3. Observed and predicted fertility across years and seasons and expressed relative to the mean fertility (.421) of the flock.

FERTILITY

SEASON AND YEAR OF LAMBING

OBSERVED FERTILITY
PREDICTED FERTILITY
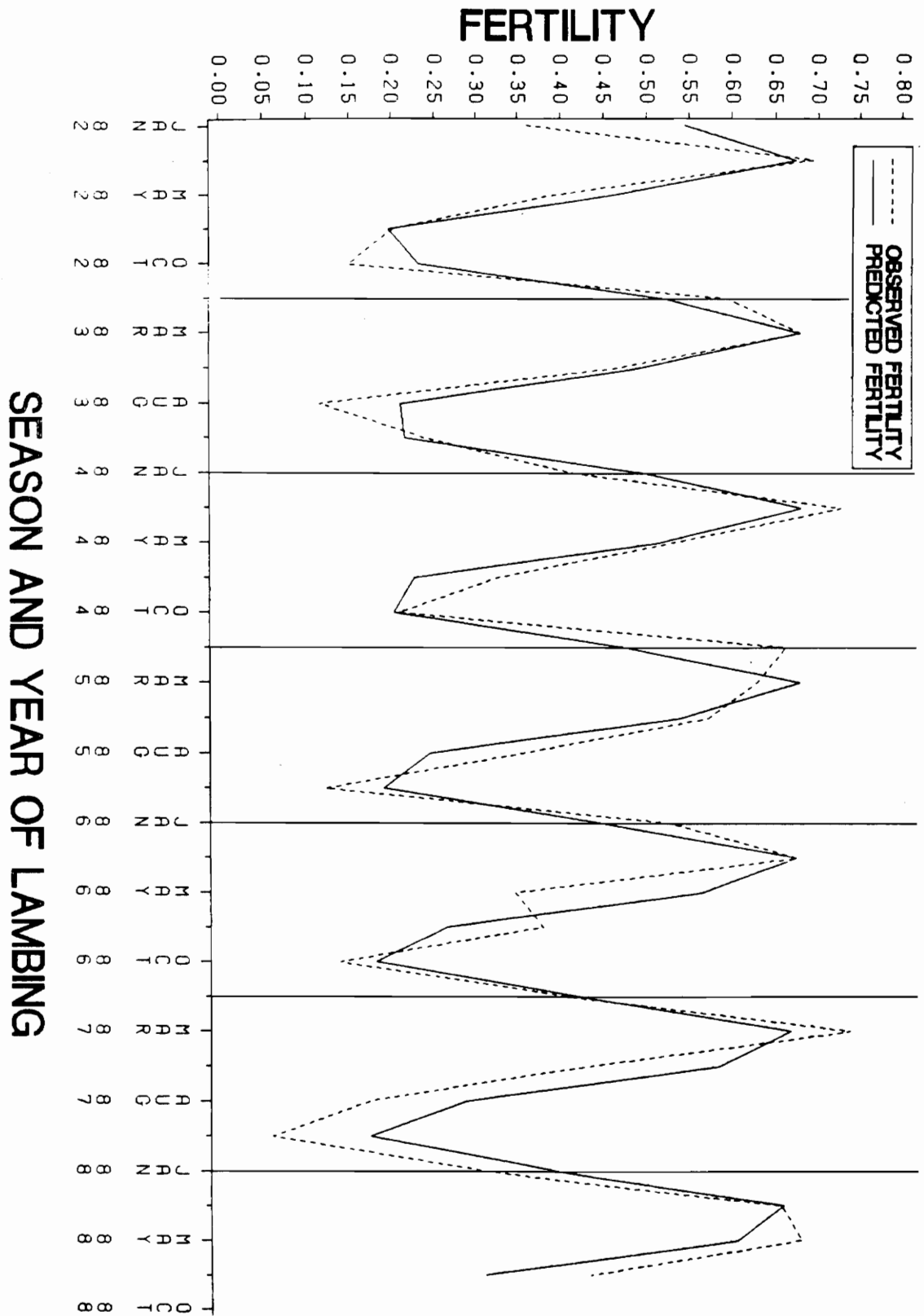
STAR Prolificacy and Days Between Lambing

Reproductive Performance of Dorset Ewes in the STAR
Accelerated Lambing System. II. Prolificacy, Days
to First Lambing and Days Between Lambings

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ABSTRACT

Prolificacy (litter size), days to first lambing and
days between lambings (DBL) were evaluated in the STAR
accelerated lambing system. The STAR system consists of
five 30-day concurrent lambing and breeding seasons starting
on January 1 (S1), March 15 (S2), May 27 (S3), August 8 (S4)
and October 20 (S5) of each year. First lambings occur at 1

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yr of age with maximal lambing incidence of 1.67 times/yr (every 7.2 mo). Records on 3,048 lambings by 1,084 Dorset ewes between 1982 and 1988 were used. Of these, 342 born in a preceding accelerated system (CAMAL) and 742 were born in STAR. Prolificacy at S1, S4 and S5 lambing resulted from exposures in favorable breeding seasons and was .11 lamb higher (P < .01) than prolificacy at S2 and S3 lambings. Annual cycles in prolificacy existed and were moderately predictable (R^2 = .45). Ewe age through 4 yr affected prolificacy (P < .10), particularly among younger STAR-born ewes (P < .001); season-specific ewe age patterns were present (P < .05). Among ewes that became pregnant at their first exposure following a prior lambing, prolificacy was lower (P < .01) for ewes that had nursed lambs than for those that had not. On average, first lambing occurred at 476 ± 5 d with 304 ± 3 d between lambings. Ewe lambs that were first exposed in S1, S4 and S5 lambed at younger ages (P < .001). Ewes that were first exposed in unfavorable seasons had more DBL (P < .001) than ewes first exposed in favorable seasons. Pregnancy and nursing status (PNS) at the previous lambing had no effect on DBL but a curvilinear relationship between age up to 4 yr and DBL was observed (P < .05). Adjustment of prolificacy records for age and PNS and of DBL for age was proposed.

(Key Words: Sheep, Dorset, Accelerated Lambing, Prolificacy, Days Between Lambing.)

Introduction

Accelerated lambing programs provide opportunities to increase lamb production by increasing the frequency of lambing. Further improvements can be incurred if litter size at each lambing is maintained at reasonably high levels. Thus the ability to lamb in different seasons and to maintain high prolificacy throughout the year are important characteristics for ewes managed in accelerated systems.

In order to assess genetic merit for a trait, environmental effects on performance must be removed. Effects of environmental factors on fertility of ewes in the STAR accelerated lambing system were considered by Lewis et al. (1990). The objective of this study was to characterize effects of ewe age, season of birth, number of seasons since last lambing and ewe pregnancy and nursing status at a previous lambing on prolificacy and days between lambings. The effect of ewe birth season and year on days to first lambing was also investigated. Lewis et al. (1990) defined fertility as a binomial trait and proposed using probabilities of conception unique to each season of exposure and ewe age to account for environmental effects on fertility. However, exposure periods differ among accelerated lambing systems, making this approach specific to a given program. Days between lambings was thus

considered to be a potentially less restrictive measure of aseasonal fertility in multiple-season lambing programs.

Materials and Methods

Data. Records from 3,048 lambings by 1,084 Dorset ewes managed under the STAR accelerated lambings system at Cornell University collected between 1982 and 1988 were used. The STAR program has five 30-d concurrent breeding and lambing seasons per year beginning on January 1 (S1), March 5 (S2), May 27 (S3), August 8 (S4) and October 20 (S5). Ewes are either lambing or exposed to a ram at each season. Optimally, a ewe could lamb every 7.2 mo beginning at 1 yr of age. Details concerning management and record-keeping for the flock have been described by Lewis et al. (1990).

Exposures in S2 (March) and S3 (May) occur when many sheep are anestrous, and will be referred to as unfavorable seasons. Exposures in S1 (January), S4 (August), and S5 (October) were considered favorable.

The STAR program was initiated in S1, 1982 with 342 ewes born in the Cornell alternate month accelerated lambing (CAMAL) system (Hogue et al., 1980; Iniguez et al., 1986). The remaining 742 ewes were born in the STAR system; their records begin in S1, 1983. Numbers of records and mean performance of these ewes in the STAR system were described

by Lewis et al. (1990).

Traits considered in this study were prolificacy (number of lambs born per ewe lambing), age at first lambing (DFL; d) and number of days between lambings (DBL). Environmental factors considered were ewe age, prolificacy and nursing status (PNS) at the previous lambing, and, for prolificacy, the interval between lambings. Age was defined as the number of seasons (S) since birth. CAMAL ewes were categorized by birth date into birth seasons comparable to those of STAR-born ewes. Interval to conception was the number of exposures (seasons) required before a ewe became pregnant. An interval of 1 corresponded with conception at the first exposure after lambing. Intervals of 5 or more seasons were grouped together; only 130 intervals exceeded five seasons. Categories for PNS (Lewis et al., 1990) included ewes that produced single or multiple lambs that did not survive (1-0 and 2-0, respectively); produced a single and nursed one or two lambs (1-1); or produced twins or triplets and nursed one (2-1) or multiple (2-2) lambs. Subclass numbers by interval and PNS are listed on table 7.

Some inbreeding was present in the ewes (Iniguez et al., 1986; Lewis et al., 1990). Inbreeding coefficients were estimated by procedures described by Quaas (1976). Ancestries of CAMAL ewes were incomplete, so inbreeding effects were considered only for STAR ewes.

<u>Prolificacy.</u>

<u>Seasonal periodicity.</u> Annual prolificacy patterns were evaluated using procedures of Stroup et al. (1987) and Lewis et al. (1990). After removal of time trends in prolificacy by linear regression, residuals for prolificacy in each year and season were analyzed with the nonlinear model:

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

where t represented consecutively numbered year-season combinations, α_1 and α_2 were regression coefficients, and A was the interval between peak prolificacies. Parameter estimates were derived using nonlinear regression procedures (SAS, 1985). Since a yearly periodicity was expected, A was either allowed to vary or was fixed at 5. The difference in residual sums of squares between these analyses was used to test the hypothesis of a yearly periodicity. Reduced models including only the sine or cosine function were also fit to test significance of α_1 and α_2.

<u>Ewe age.</u> Analysis of variance (ANOVA) models described by Lewis et al. (1990) were used to evaluate environmental effects on prolificacy. All analyses were conducted after absorption of contemporary group (ewe birth season and year) and ewe effects. Independent variables were lambing season and linear and quadratic regression coefficients of prolificacy on ewe age in seasons. Homogeneity of age

regressions among lambing seasons was also tested. The interaction of ewe age with ewe birth season was found to be unimportant in preliminary analyses and was excluded from the model. STAR and CAMAL data were either combined or considered separately; models considering both CAMAL and STAR ewes included the effect of ewe birth system and its interaction with lambing season.

Ewe birth season. Although ewe birth season was absorbed rather than fit in the overall analysis, its effect on prolificacy at first lambing was of interest. Ewe birth season completely defines first exposure season and its effect would likely be most pronounced at early lambings. Thus, data from STAR ewes that lambed first at or before an age of 9 S were analyzed with the model:

$$Y_{ijkl} = \mu_Y + B_i + R_j + S_k + (BS)_{ik} + \epsilon_{ijkl},$$

where Y_{ijkl} was the prolificacy of the lth ewe born in the ith season (B) and the jth year (R) and lambing in the kth season (S); μ_Y was the mean prolificacy and ϵ_{ijkl} was the residual error.

Interval and pregnancy and nursing status. First lambing records could not be used to evaluate the effects of interval and PNS on prolificacy. This constraint reduced the size of the data set to 1,086 STAR and 886 CAMAL records. Effects of interval and PNS were added to the ewe

age model. Effects of interval and PNS were considered only after fitting ewe age effects because ewe age was anticipated to have a direct effect on interval and PNS. The goal was thus to investigate effects of these variables that were expressed in addition to the overall age relationship. Preliminary analyses suggested that PNS effects on prolificacy were restricted to interval 1 (i.e., to ewes that conceived at their first opportunity) and that age interactions with lambing season were largely unimportant. Thus the effects of PNS were only tested within interval 1.

Adjustment factors. Because effects of interval and PNS could be estimated only for ewes that lambed at least twice, a two-stage protocol was used to derive final adjustment factors for PNS and ewe age; interval effects did not influence prolificacy. Additive adjustments for PNS within interval 1 were estimated using a model that included contemporary group, ewe and age; ewes with a PNS category of 1-1 were used as the base class.

Prolificacy records for interval 1 were then adjusted for effects of PNS prior to analysis of all records to derive linear and quadratic regression coefficients for age and to test homogeneity of regression coefficients among lambing seasons and ewe birth systems. Prolificacy was adjusted to a mature age equivalent with the formula:

adjusted $Y_{ijkl} = Y'_{ijkl} + \alpha_{1k}(M_k - X_{ijkl}) + \alpha_{2k}(M_k^2 - X_{ijkl}^2)$,

where Y'_{ijkl} was an individual prolificacy record adjusted for PNS, and α_{1k} and α_{2k} were linear and quadratic regressions prolificacy on age for lambing season k. M_k was the age of maximum prolificacy within season k and X_{ijkl} was the seasonal age of the ewe for the record. If the maximum predicted prolificacy occurred after 20 S or if no maximum was present, M was set equal to 20 S.

Inbreeding. Inbreeding effects on prolificacy were evaluated by linear regression on inbreeding coefficients within contemporary group and sire of ewe using procedures described by Lewis et al. (1990). A maximum inbreeding level of 25% occurred only for daughters of one purchased sire were excluded, leaving 1,287 STAR-born ewe records. Since inbreeding levels increased over time, effects of lambing season, year and their interaction replaced ewe age regressions to precisely define contemporary groups in the inbreeding analysis. In models that included interval and PNS (nested within interval 1), loss of data due to exclusion of first lambing records reduced the number of records to 713; the interaction of lambing year and season had to be excluded from this model due to confounding with other effects.

Days to first lambing.

In the STAR system, age at first lambing and birth season are interrelated because birth season determines the season of first exposure to a ram. To characterize this relationship, DFL for STAR ewes was analyzed using the model:

$$DFL_{ijk} = \mu_{DFL} + B_i + R_j + (BR)_{ij} + \epsilon_{ijk},$$

where μ_{DFL} was the mean DFL, DFL_{ijk} was the DFL of the kth ewe born in the ith season (B) and j^{th} year (R) and ϵ_{ijk} is residual error. Records on 1987-born ewes were removed to avoid missing year-season subclasses, leaving data on 674 lambings. Numbers of observations by ewe birth season were 259 (S1), 163 (S2), 69 (S3), 106 (S4) and 77 (S5).

Days between lambings.

Effects of season, ewe age and PNS on DBL were considered. Measurement of DBL requires at least two lambings, so only 1,086 and 886 records on STAR and CAMAL ewes, respectively, were available. These records were considered separately and together.

Subclass numbers for previous season of lambing (PSL) and PNS for STAR and CAMAL ewes are given in table 8. Due to the nature of the trait, some redefinition of fixed effects was necessary. Initial analyses were similar to

those used for prolificacy, with combined effects of PSL, ewe age and PNS fit within system, contemporary group and ewe. However, estimates for fixed effects were unreasonable, particularly for age effects. A continual increase in DBL as ewes aged with maxima at ages in excess of 7 yr was suggested. This result perhaps reflected the lower prolificacy of young ewes relative to older ewes and suggested that confounding existed between effects of PNS and ewe age. Thus, alternative models were proposed.

Season. Comparisons of seasonal differences in DBL were based on a model including PSL fit within contemporary group, ewe, and, for combined data, ewe birth system. Linear contrasts were used to test for differences in DBL between PSL classes that led to subsequent first exposures that were within (S3, S4 and S5) or outside (S1 and S2) the favorable breeding season.

Ewe age. Linear and quadratic ewe age effects were considered within PSL, year of lambing (PYL) and PNS. Simultaneous inclusion of contemporary group and ewe effects in the model was not possible. The specific model was:

$$DBL_{ijkl} = \mu_{DBL} + PSL_i + PYL_j + PNS_k + (PSL,PYL)_{ij} +$$

$$(PSL,PNS)_{ik} + (PYL,PNS)_{jk} + (PSL,PYL,PNS)_{ijk} +$$

$$\beta_1(X_{ijkl} - \mu_X) + \beta_2(X_{ijkl} - \mu_X)^2 + \epsilon_{ijkl},$$

where DBL_{ijkl} was the DBL for the lth ewe lambing in the jth year (PYL) and the ith season (PSL) and in the kth PNS class. μ_{DBL} was the mean DBL, β_1 and β_2 were linear and quadratic regression coefficients of DBL on ewe age, X_{ijkl} was the ewe's age at the record, μ_X was the mean ewe age and ϵ_{ijkl} was residual error. Records on ewes with intervals in excess of 510 d were deleted. Since age effects were expected to diminish as ewes matured, records on young (20 S and younger) and old ewes were considered separately. Only combined STAR and CAMAL data were used. Subclass regressions of age within PSL were considered, but no effect was observed, and these effects were subsequently ignored.

   Pregnancy and nursing status. A somewhat different model was used to evaluate PNS effects. Specifically:

$$DBL_{ijklmn} = \mu_{DBL} + [B_i + R_j + PSL_k + PYL_l] +$$

$$PNS_m + \epsilon_{ijklmn},$$

where DBL_{ijklmn} was the DBL of the nth ewe born in the ith season (B) and j^{th} year (R) and lambing in the kth season (PSL) and l^{th} year (PYL) and in the mth PNS class. μ_{DBL} was the mean DBL and ϵ_{ijklmn} was the residual error. All cross-classifications of terms shown in brackets were also included. Individual ewe effects could not be fit, but the absorption of ewe birth season and year, PSL and PYL allowed

detection of PNS effects independent of contemporary group and age. Linear contrasts were designed to compare effects of pregnancy status (single vs multiple), lactational status (non-lactating vs lactating), and rearing status (single vs multiple) on DBL. These contrasts were not orthogonal; significance was determined using Bonferroni critical values (Gill, 1978).

Adjustment factors. The previous analyses suggested that age adjustment of DBL was needed only for ewes less than 4 yr of age. Adjustment of DBL to a mature ewe equivalent resulted in unreasonably short DBL for ewes that performed well at young ages. Thus DBL was adjusted to a young ewe (5 S) basis as follows:

$$\text{adjusted DBL}_i = \text{DBL}_i - \alpha_1 (5 - X_i) - \alpha_2 (25 - X_i^2),$$

where DBL_i was the ith record on a ewe, α_1 and α_2 were linear and quadratic regressions of age on DBL, and X_i was the seasonal age of the ewe at the ith record. Since minimum DBL was reached at 18 S, age specific adjustments were only applied to ewes under this age. For older ewes, X_i was set at 18 S.

Inbreeding Linear effect of inbreeding on DBL were considered for STAR ewes by adding sire of ewe effects and the intrasire regression of DBL on inbreeding coefficient to

existing models. Daughters of the one sire that produced offspring with an inbreeding coefficient of 25% were excluded; 713 records were used.

Results and Discussion

Prolificacy

Seasonal effects and periodicity. Prolificacy of both STAR and CAMAL ewes bred in favorable seasons (S1, S4 and S5) was about .11 lambs higher than that observed in S2 and S3 (P < .01). Least squares constants, expressed relative to S5 lambings, were -.01 ± .04 (S1), .03 ± .04 (S2), -.13 ± .049 (S3) and -.28 ± .05 (S4). Highest prolificacy occurred at March lambings (S2), concomitant with the greater fertility observed in October exposures (Lewis et al., 1990). The greater prolificacy in October (S5) relative to May (S3) lambings was unexpected, but may have occurred in response to a flushing effect in ewes bred on early spring forages.

A marginal increase (P < .10) in prolificacy was seen across years and seasons. After removal of this trend, the periodic model defined a modest amount of remaining variation in prolificacy (R^2 = .45). The period between peak prolificacies exceeded a year (5.29 S; P < .01) suggesting that in this sample of years, some additional unknown factors were acting to affect the expected annual

periodicity . Both regressors (α_1 = -.006; α_2 = .128) were important to predict the periodicity (P < .01). When the periodicity was fixed at a cycle length of 5 S, a sinusoidal function (α_1 = .106; P < .01) alone defined cyclicity.

Unlike flock fertility (Lewis et al., 1990), predicted and actual prolificacy rarely corresponded exactly (figure 4). Although lambings from spring and summer exposures generally produced fewer lambs, the relatively poor fit implies only modest predictive capacity for these models.

Ewe age. Results of ANOVA of prolificacy, with and without the interaction of ewe age with lambing season, are shown in table 9. For CAMAL and combined data, inclusion of interactions overparameterized the model; neither the lambing season main effect or its interaction with age were significant. However, among the younger STAR ewes, seasonal effects on prolificacy appeared to be age dependent. These findings suggested that a more detailed consideration of effects of age on prolificacy among seasons was warranted.

Age effects on prolificacy among STAR and CAMAL ewes were considered by lambing season. Maximal prolificacy occurred at older ages for CAMAL ewes than for STAR ewes in all seasons except S4. This result largely reflects differences in age distributions between groups. Older CAMAL ewes appeared less sensitive to seasonal effects on prolificacy with peak prolificacy at an average age of 34.1 S. Less consistency across seasons in age at maximal

prolificacy was seen in STAR ewes. On average, STAR ewes reached maximal prolificacy by 26.6 S. In both groups, linear and quadratic age effects were most apparent for exposures in August and October. In these seasons, prolificacy increased strongly with age, perhaps indicating a heightened ability to twin within these seasons at any age.

Prolificacy appeared to effectively reach maximum levels by 20 S. No linear or quadratic age effects were observed among STAR or CAMAL ewes after 4 yr of age. ANOVA for prolificacy by ewes 20 S or younger are shown in table 10. Among CAMAL ewes, no age or season effects were apparent after adjustment for age by season interaction, but a significant linear effect was found without interaction. Significant age and season effects were observed for both STAR and combined records. Predicted mean prolificacy by lambing season for ewes 20 S and below and above 20 S are shown in table 11 with estimates of linear and quadratic regression coefficients of prolificacy on age among younger ewes.

For STAR records and combined records, effects of lambing season, age and their interaction were significant. To more clearly define the nature of the interaction, least squares constants were used to characterize pattern (figure 5), early slope (between 5 and 10 S) and ewe age at maximum prolificacy (table 11) for each season. Aging patterns and

slopes were similar among lambings from favorable exposures, although maximum prolificacy for S2 and S3 lambings (1.74 and 1.41 lambs, respectively) occurred at younger ages (about 15 S). Maximum prolificacy for S1 and S5 lambings occurred at the upper age bound of about 20 S. The increase in prolificacy with age observed for exposures in favorable seasons was approximately .4 lambs between 5 and 10 S, suggesting increasing age allows for expression of increased reproductive rate.

Age and prolificacy combine differently for exposures during unfavorable seasons. For S4 lambings, the regression equation was essentially flat through 13 S, with a gradual increase thereafter, suggesting that if young ewes settle to such exposures, they will likely produce a single.

Ewe age adjustment to a mature age ($\geq$ 20 S) appears warranted. A common adjustment for all seasons could be derived, but separate seasonal adjustments appear more accurate. Since the distinction between STAR and CAMAL ewes is specific to these data, the linear and quadratic regressions estimated from combined data (table 11) provide the most generally applicable factors. As seen in figure 6, the relationship between age and prolificacy is quite similar for combined data and for STAR data alone.

Ewe birth season. For ewes under 2 yr of age at first lambing, ewe birth year, lambing season and the interaction of ewe birth and lambing season define variation (P < .01)

in prolificacy. Ewe birth season alone was not important (P > .15). Depending on a ewe's birth season, her first exposure will occur at either a favorable or unfavorable period and Lewis et al. (1990) have shown that fertility in unfavorable seasons was low, particularly among young ewes. Since ewes born in S4 and S5 are first exposed in S2 and S3, few settle at their initial exposure. Instead, they lamb at slightly older ages from favorable exposures. Ewes born in S1 and S2 are first exposed during the favorable seasons and tend to lamb at younger ages. Since prolificacy at exposures in S1, S4 and S5 is particularly sensitive to age, age effects on prolificacy are readily detectable. Thus ewe birth season and lambing season are intimately connected in their influence on first lambing prolificacy.

Least squares means for prolificacy at first lambing by ewe birth season support this argument. Since no ewes born in S2 lambed in S4, means could only be estimated ignoring interaction. Mean prolificacy and SE by ewe birth seasons were 1.06 ± .04 (S1), 1.09 ± .05 (S2), 1.21 ± .06 (S3), 1.40 ± .05 (S4) and 1.27 ± .06 (S5). Ewes born in S1 and S2 tend to be both less prolific and to first lamb at younger ages (5.6 vs 6.8 S) than ewes born later in the year. Prolificacy at first lambing showed similar seasonal trends to those noted earlier. Least squares means by lambing season were 1.30 ± .04 (S1), 1.39 ± .03 (S2), 1.17 ± .04 (S3), .95 ± .10 (S4) and 1.23 ± .09 (S5). Since minimum

prolificacy is 1.0, the mean prolificacy at S4 is an artifact of the model.

Interval and PNS. The number of seasons since last lambing was found to have no effect on prolificacy. Lewis et al. (1990) reported that fertility was reduced in ewes re-exposed shortly after weaning, but there is apparently no similar effect on prolificacy in ewes that conceive.

Overall PNS effects were important (P < .01), but when each interval was considered separately, PNS was important only for ewes within interval 1. Least squares constants for PNS effects (relative to PNS 1-1) within interval 1 were .01 ± .10 (1-0), -.06 ± .14 (2-0), -.30 ± .08 (2-1) and -.25 ± .05 (2-2). Ewes that did not lactate at their previous lambing were less fertile (Lewis et al., 1990), but those that did conceive were less prolific if they had raised a lamb. Adjusting prolificacy for PNS effects within interval 1 thus appears warranted.

With PNS effects nested within interval 1, interval remained unimportant (P > .40). To accommodate nesting of PNS effects within interval 1, a least squares mean for prolificacy in interval was calculated as a weighted mean of the PNS constants. Constants for the other intervals were then expressed as a deviation from interval 1 and were -.02 ± .05, .04 ± .05, .14 ± .07 and .05 ± .08 for intervals 2, 3, 4 and 5 or more, respectively. The depressed prolificacy relative to interval 4 associated with long intervals

suggests an overall reduction in fitness among chronically infertile ewes. Overall, no correction for interval was indicated by these data.

   Adjustment factors. Additive adjustment constants for PNS within interval 1 were constructed by reversing the sign of the least squares constants. Before and after applying PNS adjustments, mean prolificacies were 1.58 and 1.58 (1-0; SE: .08), 1.62 and 1.69 (2-0; SE: .10), 1.54 and 1.84 (2-1; SE: .06), and 1.63 and 1.86 (2-2; SE: .04), respectively. Since adding a constant does not change variance, SE did not differ between adjusted and unadjusted data. Adjusted prolificacies ranged between .99 and 3.30 lamb. The larger adjusted prolificacies for ewes that twinned and raised one or more lambs at their previous lambing imply that these ewes would have been even more prolific at their current lambing had their previous performance not held them back.

   Linear and quadratic subclass regressions of age on PNS-adjusted prolificacy through 20 S by lambing season were .1200 and -.0029 (S1), .1482 and -.0040 (S2), .1171 and -.0029 (S3), -.0532 and .0036 (S4), and, .0467 and -.0003 (S5), respectively. For lambings from favorable exposures, these correspond with maximum prolificacies at 20.7 (S1), 18.5 (S2), and 20.2 (S3). A minimum prolificacy at 7.3 S for S4 lambings and at unreasonably advanced ages for S5 lambings were also implied. To evaluate the efficacy of the age correction, ages were grouped into 5 season increments

(5 to 9 S, 10 to 14 S, 15 to 19 S, and 20 S or more) and adjusted mean prolificacies calculated; values were 1.84 ± .01, 1.80 ±   .02, 1.75 ±   .02 and 1.76 ±   .02, respectively. Prolificacies on young ewes may be slightly over-corrected. Little residual variation remained once the age adjustments were applied (P > .20), but specific relationships among age, lambing season and prolificacy may still exist.

Since season-specific ewe age regressions are unique to the seasons defined in these data, linear and quadratic regression coefficients across seasons also were estimated. They were .1149 and -.0027, respectively, and correspond with a maximal prolificacy at about 21.3 S, slightly beyond the upper age bound on the data.

Inbreeding.   Inbreeding levels within the flock were mild;   most ewes had inbreeding coefficients of less then .0625.   Within this range, no inbreeding effects (P > .30) were observed, either with or without inclusion of effects of interval and PNS.

Days to first lambing

First lambing by STAR ewes occurred at an average of 476 ± 5 d of age.   Ewe birth season and year (both P < .01) and their interaction (P < .05) influenced DFL.   Within ewe birth seasons,   DFL reflected whether early exposures occurred during favorable or unfavorable seasons. Ewes born in S1, S2 and S3 had first exposures during favorable

seasons and had fewer DFL (P < .001) than ewes born in S4 and S5. Least squares means for DFL by ewe birth season were 458 ± 9 (S1), 436 ± 13 (S2), 466 ± 20 (S3), 537 ± 16 (S4) and 495 ± 16 d (S5). After an initial decrease in DFL from 507 ± 15 to 444 ± 14 d among ewes born in 1982 and 1984, respectively, DFL increased to 499 ± 13 d in ewes born in 1986.

Days between lambings.

Season. Averages for DBL for STAR, CAMAL and combined data by PSL are shown in table 12. Since PSL defines the season at which a ewe was next exposed, average DBL for PSL of S1 and S2 was larger (P < .001) than for the other seasons. Differences in DBL between previous lambings that led to exposures in favorable vs unfavorable seasons were greater among CAMAL ewes. The mean difference between favorable and unfavorable seasons was 42.9 ± 8.6 d for CAMAL ewes but only 33.9 ± 7.6 d for STAR ewes. On average, ewes lambed every 304.6 ± 2.8 d.

Ewe age. Linear and quadratic age effects on DBL were significant for both STAR and CAMAL ewes. Linear and quadratic regression coefficients were -8.154 and .214, respectively, for STAR data, and - 3.260 and .048, respectively, for CAMAL data. Minimum DBL were observed at 19.1 (STAR) and 34.2 S (CAMAL). Regression coefficients for the combined data were -4.119 (linear) and .066 (quadratic)

and defined a minimum DBL at 31.2 S.

The shapes of these age curves were similar, all suggesting a relatively rapid increase in DBL beyond the age minimum. This result seemed curious, since an ever-increasing DBL as ewes mature was not expected and was thus perhaps an artifact of fitting the quadratic term. Study of partitions of records based on age supported this thesis. For combined STAR and CAMAL data, no age effects (P > .2) on DBL were found among ewes greater then 20 S. Below this age, a curvilinear relationship (P < .001 for linear term; P < .05 for quadratic term) was observed. Linear and quadratic regression coefficients were -8.992 and .247, respectively, for ewes below 20 S. These findings suggest that DBL among ewes 4 yr and younger should be adjusted for age.

The efficacy of the age adjustments were considered by comparing mean DBL across age categories. As with prolificacy, adjusted mean DBL were calculated for ewes 5 to 9 S, 10 to 14 S, 15 to 19 S and 20 S or older and were 317.7 ± 2.9, 321.5 ± 3.6, 314.0 ± 4.1, and, 318.5 ± 3.1, respectively. Adjusted DBL ranged from 173.0 to 553.0. Although DBL in the 15 to 19 S age group appeared low, little residual variation associated with age remained after adjustment (P > .55).

Pregnancy and nursing status. PNS status at the lambing initiating an interval only defined variation in DBL

among STAR ewes (P < .05). No effect was observed for CAMAL ewes (P > .45) or combined data (P > .10). For STAR data, ewes that lactated (PNS of 1-1, 2-1 and 2-2) had 32.3 ± 12.1 d shorter lambing intervals (P < .05) than ewes that did not lactate (PNS of 1-0 and 2-0). These findings support the observation of Lewis et al. (1990) that ewes that lactated at their previous lambing tended to be more fertile.

Relative to a PNS of 1-1, least squares constants for PNS effects for STAR ewes were 29.6 ± 14.1 (1-0), 31.2 ± 18.2 (2-0), -12.0 ± 11.2 (2-1) and 6.4 ± 7.5 (2-2) d. Although these constants could be used to adjust for PNS, but such a correction would be of doubtful utility and was not confirmed in CAMAL ewes. Since ewes that twin and lactate appear to have the shortest DBL, a favorable adjustment (i.e., a reduction in DBL) would be applied to less fecund ewes. Such a correction cannot currently be easily justified on biological grounds.

Inbreeding. No inbreeding effect on DBL was found (P > .80).

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TABLE 7. SUBCLASS NUMBERS BY INTERVAL TO CONCEPTION
AND BY PREGNANCY AND NURSING STATUS FOR EWES BORN
IN EACH ACCELERATED LAMBING SYSTEM

	Accelerated lambing system in which ewe was born	
Subclass	STAR	CAMAL
Interval[a]		
1	433	376
2	281	246
3	230	162
4	84	55
5 or more	58	47
PNS[b]		
1-0	56	47
1-1	550	389
2-0	33	28
2-1	98	87
2-2	349	335

[a]Number of seasons since preceding lambing.

[b]Pregnancy and nursing status were: produced single and
multiple lambs that did not survive (1-0 and 2-0, respectively);
produced a single and nursed one or two lambs (1-1); or produced
twins or triplets and nursed one (2-1) or multiple (2-2) lambs.

TABLE 8. SUBCLASS NUMBERS FOR ANALYSIS OF DAYS BETWEEN LAMBINGS FOR PREVIOUS LAMBING SEASON, PREGNANCY AND NURSING STATUS AND THE ACCELERATED LAMBING SYSTEM IN WHICH THE EWES WERE BORN

	Accelerated lambing system in which ewe was born	
Subclass	STAR	CAMAL
PSL[a]		
1	329	324
2	380	253
3	137	110
4	141	107
5	99	92
PNS[b]		
1-0	56	47
1-1	550	389
2-0	33	28
2-1	98	87
2-2	349	335

[a]Previous season of lambing. Season starting dates were: 1 - January 1; 2 - March 15; 3 - May 27; 4 - August 8; 5 - October 20.

[b]Pregnancy and nursing status were: produced single and multiple lambs that did not survive (1-0 and 2-0, respectively); produced a single and nursed one or two lambs (1-1); or produced twins or triplets and nursed one (2-1) or multiple (2-2) lambs.

TABLE 9. MEAN SQUARES FROM THE ANALYSES OF VARIANCE OF
PROLIFICACY AFTER ABSORPTION OF EFFECTS OF EWE BIRTH
SYSTEM, YEAR AND SEASON AND OF EWE

Source[a] df[b]		STAR		CAMAL		Combined	
		W/O[c]	With[c]	W/O[c]	With[c]	W/O[c]	With[c]
S	4	5.74***	.35	.95**	.50	5.17***	.53+
Age							
Linear	1	19.29***	6.36*	14.12***	3.16***	51.17***	19.35***
Quad	1	5.84***	1.85***	7.59***	1.72*	22.26***	9.30***
Age X S							
Linear	4		.94**		.48		.59+
Quad	4		1.10**		.32		.34
S X sys	4					.70*	1.20***
Residual[d]		.26	.25	.26	.26	.26	.26
R^2		.54	.55	.39	.40	.48	.49

[a]S is lambing season and sys is the accelerated lambing system in which the ewe was born. Age is expressed in seasons since birth.

[b]Degrees of freedom.

[c]Refers to model without (W/O) and with age by season interactions.

[d]Residual degrees of freedom across columns were 1,080, 1,072, 880, 872, 1,962 and 1,954, respectively.

+P < .10.
*P < .05.
**P < .01.
***P < .001.

TABLE 10. MEAN SQUARES FROM ANALYSES OF VARIANCE OF PROLIFICACY
AMONG EWES 4 YR OF AGE AND YOUNGER AND AFTER ABSORPTION OF
EWE BIRTH SYSTEM, YEAR AND SEASON AND OF EWE

Source[a] df[b]		STAR		CAMAL		Combined	
		W/O[c]	With[c]	W/O[c]	With[c]	W/O[c]	With[c]
S	4	5.17***	.47$+$	.07	.12	1.53***	.57*
Age							
Linear	1	13.76***	3.32***	1.80**	.21	15.75***	3.24***
Quad	1	5.84***	1.38*	.58$+$	.05	6.19***	1.05*
Age X S							
Linear	4		.82*		.05		.61*
Quad	4		.67*		.02		.48*
S X sys	4					1.02***	1.12***
Residual[d]		.23	.23	.19	.19	.22	.22
R^2		.58	.58	.61	.62	.58	.59

[a]S is lambing season and sys is the accelerated lambing
system in which the ewe was born.   Age is expressed in seasons
since birth.

[b]Degrees of freedom.

[c]Refers to model without (W/O) and with age by season
interactions.

[d]Residual degrees of freedom across columns were 935, 927,
330, 332, 1,267 and 1,259, respectively.

$+$P < .10.

*P < .05.

**P < .01.

***P < .001.

TABLE 11. MEAN PROLIFICACY BY AGE GROUP AND REGRESSION
COEFFICIENTS, LINEAR SLOPE BETWEEN 5 AND 10 S AND AGE
OF MAXIMAL PROLIFICACY AMONG EWES 4 YR AND YOUNGER

Age[a] (S)	Measure	System[b]	Lambing season					
			1	2	3	4	5	Combined
≤ 20	Mean[c]	STAR	1.522	1.556	1.333	1.115	1.438	1.483
		CAMAL	1.340	1.347	1.358	1.250	1.403	1.467
		Combined	1.407	1.437	1.266	1.059	1.377	1.444
	Linear[d]	STAR	.1376	.1843	.1609	-.0730	.0592	.1320
		CAMAL	.0630	.0906	.0941	-.0753	.1073	.0921
		Combined	.1255	.1497	.1261	-.0618	.0562	.1189
	Quad[d]	STAR	-.0036	-.0059	-.0057	.0039	-.0014	-.0037
		CAMAL	-.0011	-.0014	-.0016	.0021	-.0027	-.0019
		Combined	-.0032	-.0042	-.0038	.0032	-.0012	-.0031
	Slope	STAR	.0837	.0951	.0756	.0145	.0383	.0765
		CAMAL	.0460	.0702	.0696	-.0432	.0661	.0636
		Combined	.0779	.0869	.0697	.0131	.0381	.0724
	Maxima	STAR	19.15	15.49	14.14	9.63[e]	21.20	17.84
		CAMAL	27.78	33.25	28.80	17.63[e]	19.56	23.80
		Combined	19.78	17.87	16.75	9.51[e]	23.38	19.37
> 20	Mean[c]	STAR	1.313	1.732	1.492	1.346	1.586	1.678
		CAMAL	1.630	1.656	1.467	1.365	1.504	1.484
		Combined	1.571	1.659	1.449	1.342	1.482	1.664

[a]Records on ewes 4 yr and younger (≤ 20 S) and above 4 yr.
[b]Ewes born in the STAR or CAMAL accelerated lambing systems.
[c]Means based on least squares constants. For ≤ 20 S, means
represent prolificacy at average age within the age group,
namely: 10.13 S (STAR); 13.76 (CAMAL); and 11.11 (Combined).
[d]Linear and quadratic regression of age on prolificacy.
[e]Minimum.

TABLE 12. MEANS AND SE FOR NUMBER OF DAYS BETWEEN LAMBINGS
BY PREVIOUS LAMBING SEASON AND ACCELERATED LAMBING SYSTEM
IN WHICH THE EWE WAS BORN

Previous[a] lambing season	Accelerated lambing system in which the ewe was born		
	STAR	CAMAL	Combined
1	316.2 ± 6.5	329.5 ± 7.8	322.8 ± 5.1
2	326.7 ± 3.4	314.4 ± 6.8	325.8 ± 3.4
3	315.6 ± 11.4	282.3 ± 12.9	300.8 ± 8.6
4	235.9 ± 6.2	244.4 ± 9.4	239.6 ± 5.3
5	267.7 ± 9.2	255.7 ± 12.6	261.9 ± 7.7

[a]Previous season of lambing. Season starting dates were: 1
- January 1; 2 - March 15; 3 - May 27; 4 - August 8; 5 - October
20.

104

Figure 4. Observed and predicted prolificacy across years and seasons and expressed relative to the mean prolificacy (1.483) of the flock.

PROLIFICACY

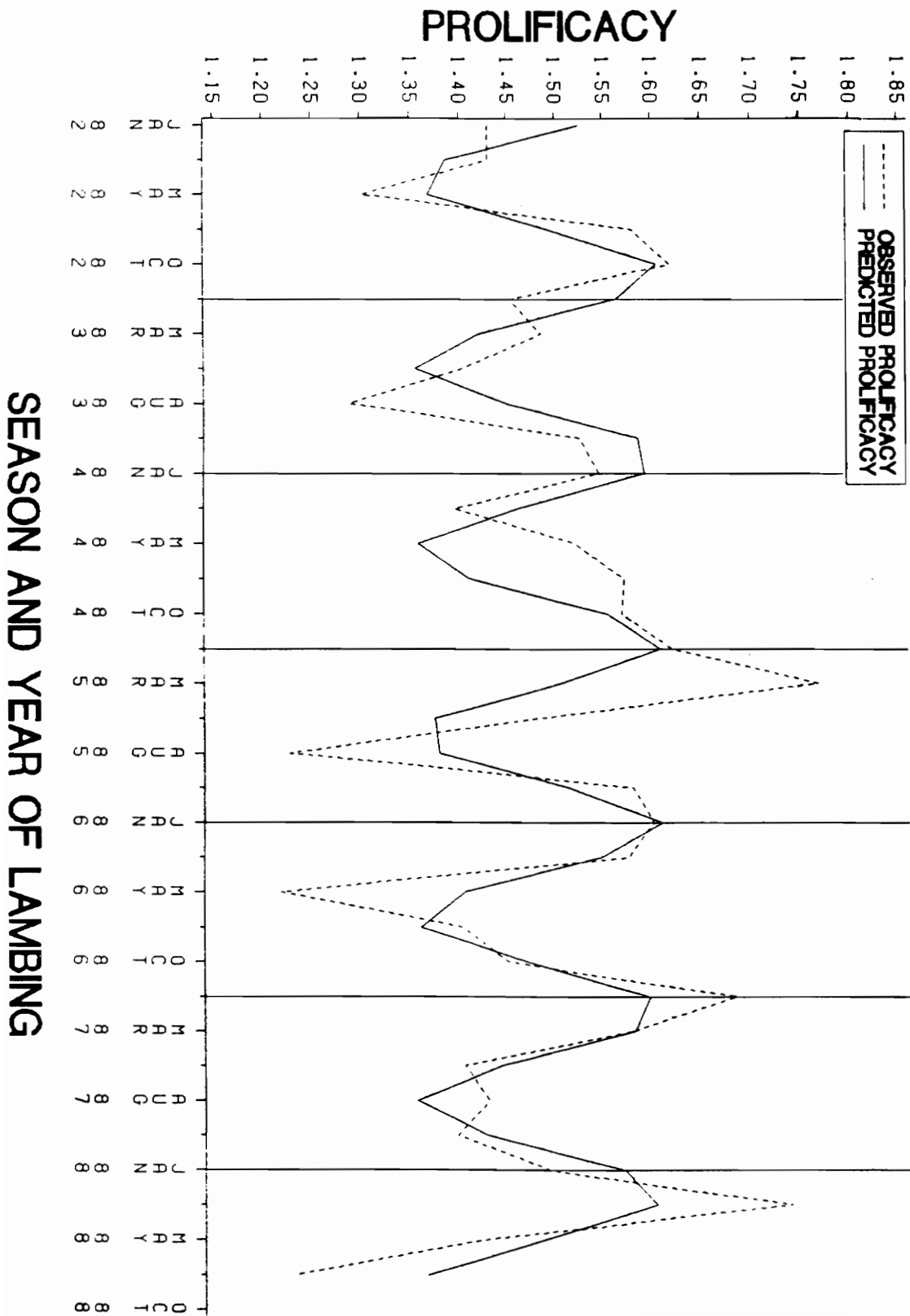SEASON AND YEAR OF LAMBING

OBSERVED PROLIFICACY
PREDICTED PROLIFICACY

Figure 5. Age effects within lambing season on prolificacy among STAR ewes 4 yr of age and younger. Differences in mean prolificacy among lambing seasons have been removed to clarify interaction between age and lambing season.
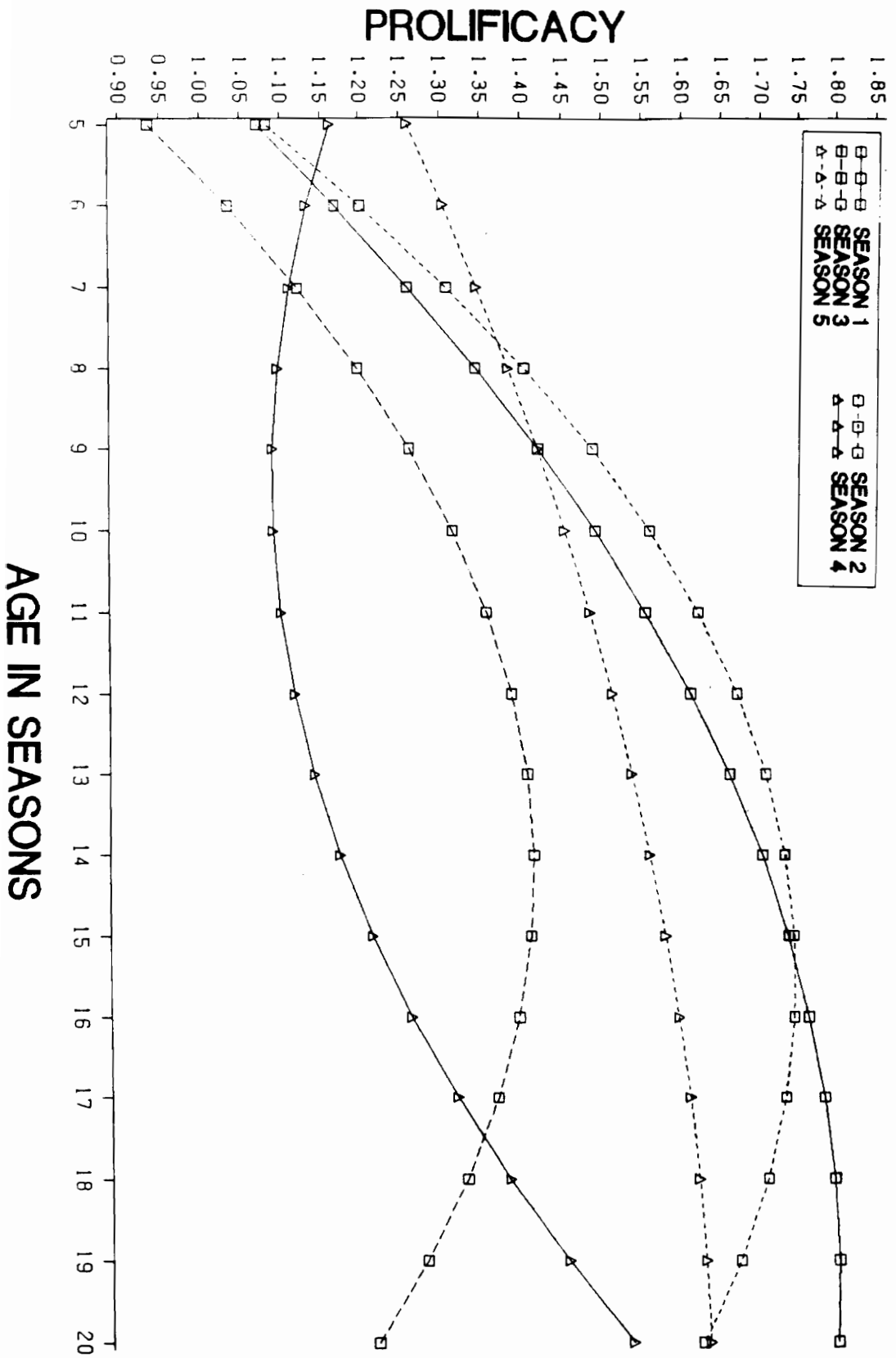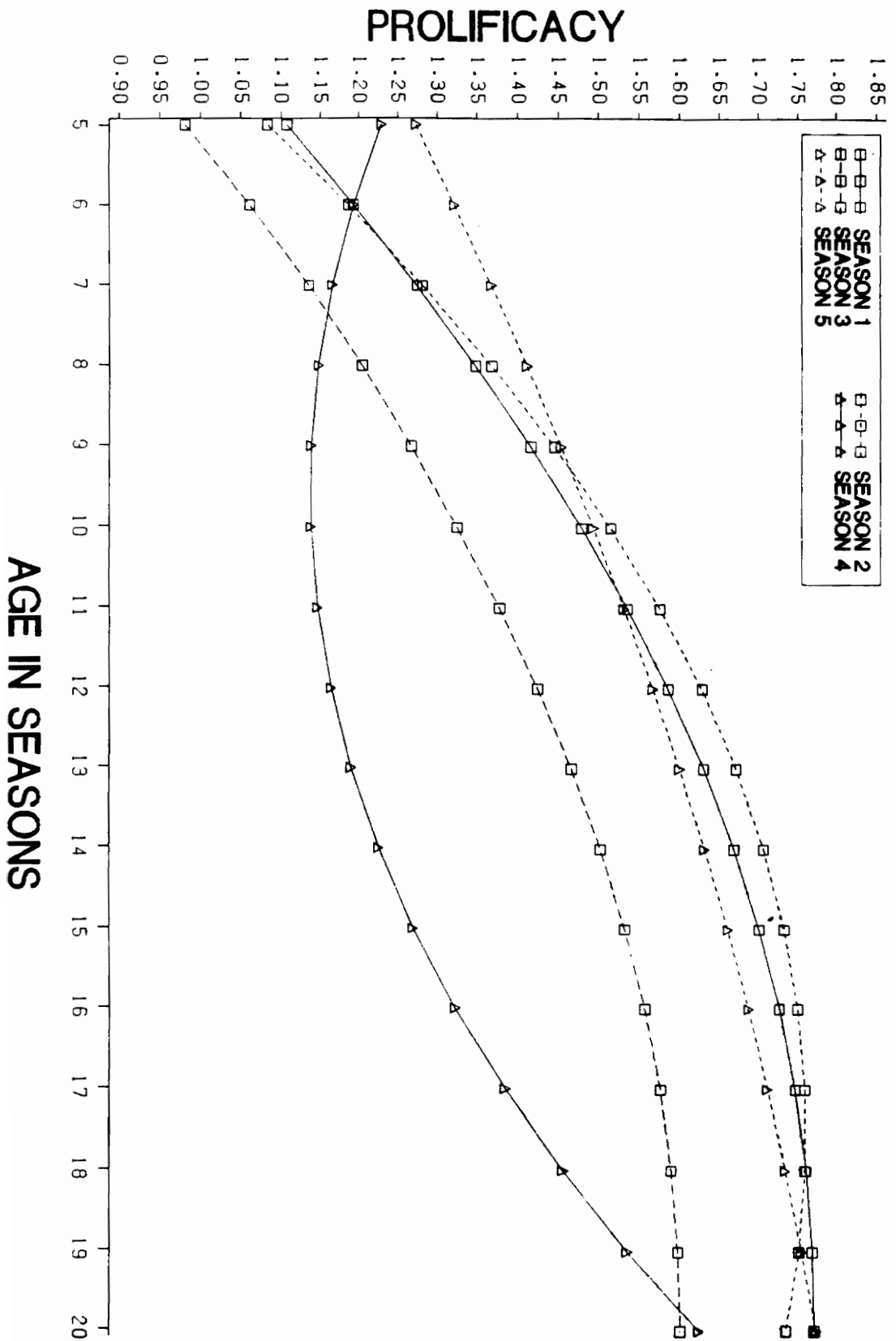
PROLIFICACY

AGE IN SEASONS

Figure 6. Age effects within lambing season on prolificacy among combined STAR and CAMAL ewes 4 yr of age and younger. Differences in mean prolificacy among lambing seasons have been removed to clarify interaction between age and lambing season.

Reproductive Performance of Dorset Ewes in the STAR
Accelerated Lambing System. III. Heritability
and Repeatability of Reproductive Traits[1]

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ABSTRACT

Heritabilities (h[2]) and repeatabilities for ewe
fertility (scored 1 or 0 for ewes that did or did not lamb
from an exposure), prolificacy, days between lambings (DBL),

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and days to first lambing (DFL; h^2 only) were estimated from data on 1,084 Dorset ewes managed in the STAR accelerated lambing system between 1982 and 1988. In the STAR system, ewes are either in breeding or lambing during five 30-d periods starting on January 1, March 15, May 27, August 8 and October 20. Preceding genetic evaluations, fertility data were transformed to an underlying liability scale based on expected fertility rates for a given age group and reproductive history. Prolificacy was preadjusted for age and for pregnancy and nursing status at the previous lambing and DBL was adjusted for ewe age. Variance components were estimated by least-squares (LS) and restricted maximum likelihood (REML) procedures. Heritabilities for fertility at first exposure were .052 ± .066 and .014 ± .101 for LS and REML, respectively; no significant sire effects were observed. At first post-lambing exposure, h^2 was .191 ± .088 (LS) and .200 ± .132 (REML), suggesting that selection should be based on fertility at older ages. For prolificacy, additive effects were detected (P < .01) at both first and second lambing. Heritabilities ranged from .158 ± .144 to .210 ± .137. Genetic variation in DFL (P < .05), perhaps indicative of additive effects on age of puberty, and DBL (P < .001) was found. DFL and DBL may provide useful alternatives to fertility as measures of aseasonality. Although intrasire variation among ewes was detected for prolificacy (P < .001) and DBL (P < .05),

repeatability estimates were low and smaller then h^2. This result suggests an antagonism between consecutive reproductive events.

(Key Words: Heritability, Repeatability, Fertility, Prolificacy, Days to First Lambing, Days Between Lambings)

Introduction

Estimates of heritability and repeatability for ewe fertility and prolificacy in annual and accelerated lambing programs tend to be low (Turner, 1969, Shelton and Menzies, 1970; Eijke, 1975; Gabina, 1989), although repeatable performance within specific seasons has been observed (Notter, 1981). Since reproductive competency at each season is necessary in accelerated lambing programs, identification of the extent of genetic control of performance across seasons was of interest.

The objectives of this study were to estimate the heritability (h^2) and repeatability of ewe fertility, prolificacy, days between lambings (DBL) and days to first lambing (DFL; h^2 only) for Dorset ewes managed under the STAR accelerated lambing program. Since fertility was defined as a binomial, all-or-none trait, a scale transformation to remove dependencies between the incidence of fertile exposure and variance estimates was also proposed.

Materials and Methods

Data.

Records on 1,084 Dorset ewes collected between 1982 and 1988 were used and included 7,269 exposures and 3,048 lambings. The flock had been managed in the Cornell University STAR accelerated lambing system which consists of five 30-d concurrent breeding and lambing seasons starting on January 1 (S1), March 5 (S2), May 27 (S3), August 8 (S4) and October 20 (S5) of each year. At each season, ewes are either lambing or exposed to a ram. Ewes are first bred at 7 to 8 mo, allowing for first lambing at 1 yr of age. At maximum, a ewe could lamb every 7.2 mo.

The STAR system was initiated with 342 ewes born in the Cornell alternate month lambing (CAMAL) system. (Hogue et al., 1980; Iniguez et al., 1986). The remaining 742 ewes were born in STAR. The flock was managed in three single-sire breeding groups. Most sires came from within the flock and were selected from prolific and(or) multiple-season lambing ewes. Rams were related both through paternal and maternal ancestries. Lewis et. al. (1990a) described specific management and breeding characteristics of the flock.

In describing reproductive performance of ewes in the STAR system, several nongenetic factors were considered (Lewis et al., 1990a, b). Ewe age was the number of

exposure seasons (S) since birth, with a ewe that was 1 yr old being a 5 S. Lambing number was occasionally used as a proxy for ewe age, with fourth and later lambings combined into a single category. Early lambing records were not available for CAMAL ewes, so a lambing number at their first record was assigned based on their age (Lewis et al., 1990a). Exposure interval defined the number of seasons after lambing before a ewe became pregnant. An interval of 1 defined a pregnancy at first post-lambing exposure. Intervals of 6 or more were grouped together. A ewe's pregnancy and nursing status (PNS) at her previous lambing was classified based on the numbers of lambs born and raised to weaning.

Ewe fertility at each exposure was defined as 1 or 0 depending upon whether a ewe did or did not lamb. In some analyses, fertility was considered relative to the previous season of lambing, which required exclusion of first exposure data. Prolificacy was defined as the number of lambs born and scored 1, 2 or 3. Preceding genetic evaluation, prolificacy was adjusted to a mature ($\geq$ 4-yr-old) ewe basis. For ewes that conceived at their first exposure season, prolificacy was also adjusted for PNS. DBL was adjusted only for ewe age. Only DBL records of 510 d or less (i.e., less than six seasons between lambing and pregnancy) were used. Adjustment factors were described by Lewis et al. (1990b).

Statistical procedures.

Fertility. Ewe fertility was expressed as a binomial (0 or 1) trait. Variance components can be estimated on the zero-one scale but are then dependent on the mean fertility at each exposure (Lush et al., 1948; Robertson and Lerner, 1949; Dempster and Lerner, 1950). Falconer (1965, 1967) suggested transforming incidence data to a liability scale to remove dependencies between mean incidence and environmental variation. The transformation assumes that a continuous, normally distributed underlying variate, termed the liability, is associated with the dichotomous phenotypic expression of the trait (Dempster and Lerner, 1950). The relationship of observed incidence with liability is defined by a fixed threshold along the liability scale such that those individuals exceeding the threshold express the trait while those below the threshold do not.

Applying these premises, fertility data were expressed on a liability scale using the expected performance of ewes of comparable ages and reproductive history. These expectations were based on transition probabilities (TP) or the estimated probability that a ewe would lamb from an exposure. Separate TP for previous lambing season, lambing number, and exposure interval combinations were used. Season of first exposure was substituted for previous lambing season for ewe lambs. Procedures for deriving TP and specific values were given by Lewis et al. (1990a).

Figures 7 through 9 show an application of the liability transformation. For STAR-born ewes that first lambed in S1 with subsequent exposure in March (S2) at an interval of 1, 22.8% were expected to become pregnant (figure 7). This proportion corresponds to a threshold at .7458 σ above the mean of a normal distribution. To adjust for specific effects of lambing year, an expected threshold based on TPs for all ewes exposed in a given year-season combination and weighted by the number and types of ewes present was calculated. This expectation was compared to the observed mean fertility for all ewes present at a particular year and season, and the difference between the predicted and observed threshold was calculated. For S4, 1986 lambings, the observed mean fertility was 38.0% while the expectation for S4 was 24.4%; these values correspond to thresholds at .3047 σ and .6554 σ, respectively, to give a threshold deviation of −.3507 σ for this year-season combination (figure 8). This implies that in 1986 more ewes became pregnant than expected for S2 exposures.

The year-season threshold deviation was then added to the expected threshold defined for each ewe by her appropriate TP, as defined by previous lambing season, lambing number and exposure interval (see table 4 of Lewis et al, 1990a). For STAR-born ewes first lambing in January (S1), 1986, the expected threshold was .7458 σ (figure 7) and the year adjusted-threshold was .3951 σ (.7458 σ − .3507

σ; figure 9). The ordinate (Y) of the standard normal distribution curve at the threshold (Snedecor and Cochran, 1980) is:

$$Y = (1/\sqrt{2\pi})\, e^{-X^2/2} \; ,$$

where e is the exponential function and X is the threshold value. A mean phenotypic value (Falconer, 1965) for each ewe was then calculated as $A = Y/P$ for ewes that lambed and $N = -[Y/(1-P)]$ for ewes that did not, and where P was the probability of fertility given the adjusted threshold. For the given example (figure 9), Y, P, A, and N equal .3690, .346, 1.0665 σ and −.5642 σ, respectively.

Heritability and repeatability estimation. Least-squares (Harvey, 1988) procedures were used to analyze the reproductive traits with the nested model:

$$Y_{ijk} = \mu + F_i + S_j + I_{jk} + \epsilon_{ijk} \; ,$$

where Y_{ijk} was the adjusted record of the kth ewe (E) in the ith year-season (F) and with the jth sire (S). μ was the mean of the adjusted records and ϵ_{ijk} was residual error. For fertility and prolificacy, the contemporary year-season was that associated with the exposure or lambing record, respectively. For DFL and DBL, it represented the ewe lamb's birth year and season or the lambing year and season initiating the interval between lambings, respectively.

For fertility, only records at the first postweaning exposure season (or first exposure season for ewe lambs) were used. Only sires with at least two daughters were included.

Estimates of heritability (h^2) and repeatability (t) were obtained from analysis of variance as:

$$h^2 = 4\sigma_S^2 / (\sigma_S^2 + \sigma_I^2 + \sigma_e^2)$$

$$t = (\sigma_S^2 + \sigma_I^2) / (\sigma_S^2 + \sigma_I^2 + \sigma_e^2),$$

where σ_S^2, σ_I^2 and σ_e^2 were variances components for sires, ewes within sires and error, respectively. Variance components were estimated by equating mean squares to their expectations which were:

$$\sigma_S^2 = (1/4)\sigma_g^2$$

$$\sigma_I^2 = (3/4)\sigma_g^2 + \sigma_{pe}^2$$

$$\sigma_e^2 = \sigma_{te}^2,$$

where σ_g^2, σ_{pe}^2 and σ_{te}^2 are variances due to additive genetic, permanent environmental and temporary environmental effects, respectively.

In some analyses, a single record per ewe was used for h^2 estimation. When this was done, the between-ewe term was

excluded from the model and the expectation of residual variance became $(3/4)\sigma_g^2 + \sigma_{pe}^2 + \sigma_{te}^2$.

Kennedy et al. (1988) noted that estimates of additive genetic variance and h^2 may be biased if inbreeding and relationships among sires were ignored. To incorporate additive relationships among sires into analyses using only one record per ewe, the least-squares model was redefined as:

$$Y_{ijk} = \mu + F_i + S_j + \epsilon_{ijk},$$

with $E(Y_{ijk}) = \mu + F_i$ and

$$Var \begin{bmatrix} s \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_s^2 & 0 \\ 0 & I\sigma_e^2 \end{bmatrix},$$

where A was the numerator relationship matrix among sires (Quaas, 1988) and I was an identity matrix. s and e were random vectors of sire transmitting abilities and residual effects, respectively. The mixed model equations were:

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1}\alpha \end{bmatrix} \begin{bmatrix} \hat{f} \\ \hat{s} \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix},$$

where X and Z were, respectively, design matrices for f and s effects, respectively, and $\alpha = \sigma_e^2/\sigma_s^2$. A^{-1} (accounting for inbreeding) was calculated using an algorithm described by Quaas (1976). Sire and residual error variance components were estimated using a restricted maximum likelihood (REML) algorithm (VanRaden, personal communication), following absorption of year-season effects.

Results and Discussion

Ewe fertility. No objective method for evaluating the expression of fertility on the underlying liability scale was apparent. Generally, phenotypic values for ewes that became pregnant to exposures during unfavorable seasons (S2 and S3) and at early lambing numbers (1 and 2) had larger positive fertility records. If such ewes failed, their negative deviations from the mean tended to be smaller. These findings are appropriate since they imply that ewes that perform under adverse environmental conditions are given credit for superior performance. Conversely, if such ewes fail, they are not as severely penalized as older ewes or ewes exposed in more favorable seasons (S1, S4, and S5).

In table 13, mean squares and their expectations for random effects are shown for fertility at first exposure (STAR-born ewes only), at first post-lambing exposure and for all exposures. From least-squares analyses, sire

effects were significant for first post-lambing exposure and for all exposures but not for first exposures. No additional ewe effects were found when considering repeated measures of fertility on individual ewes. The sire variance component from REML procedures differed from zero only for first post-lambing exposures. Heritability estimates from least-squares and REML procedures were similar.

Genetic variation in fertility at first exposure was not detected in these data. Lewis et al. (1990a) reported that young ewes were particularly sensitive to seasonal effects. Even with fertility expressed on a more continuous scale in order to give young ewes additional credit for becoming pregnant during unfavorable seasons, few 7 to 8 mo old ewes were able to conceive during March (13.1%) and May (11.7%) exposures. At favorable exposures, a larger proportion of ewe lambs became pregnant. Apparently, seasonal constraints were so overbearing that genetic variation at first exposure, if present, was not expressed. Following first lambing, heritabilities for fertility increase, suggesting that once ewes have lambed for the first time, additive effects on fertility are more readily assessed. Although delaying selection decisions until ewes reach older ages would slow the rate of response, a reasonable proportion of animals must have the capability to express the trait before selection can be practiced.

The repeatability of fertility did not differ from zero

and was lower than heritability. This result suggests that fertility at one season may be negatively associated with ewe's ability to become pregnant at other seasons. Although PNS status at the previous lambing was not accounted for in the TP, ignoring PNS would not explain the imperfect repeatability; ewes that failed to lactate had lower fertility (Lewis et al., 1990a). Shelton and Menzies (1970) reported a repeatability of -.006 among range Rambouillet ewes and suggested that under conditions of suboptimal nutrition, there may be a tendency for alternate year lambings. Notter (1981) found that a few ewes with extended intervals defined an appreciable amount of between-ewe variation for conception rate. When such data were excluded, repeatability decreased. Since 130 ewes in this study had intervals in excess of five seasons, the repeatability of fertility may even be overestimated.

Prolificacy. Table 14 shows mean squares and expected values for random effects for prolificacy at first lambing (STAR-born ewes only), second lambing and all lambings. Sire variation (P < .01) in prolificacy was observed for each trait. Heritability estimates based on variance components from least-squares and REML were similar for first and second lambing and ranged from .158 ± .144 to .210 ± .137. These values are somewhat higher than previous estimates for single lambing records (Rendel, 1956; Shelton and Menzies, 1970; Eijke, 1975).

The lower heritability estimate from data including all lambings is difficult to interpret. Turner (1969) noted that addition of yearling ewe lambing records to data used to estimate heritability resulted in significantly lower heritability values. This result could either be due to imperfect repeatability between first and later records, likely dependent on the frequency of twinning among yearling ewes, or reduced additive variation in ewe lambs. The comparatively higher least-squares and REML heritability estimates of prolificacy at first lambing would suggest that additive variation was present.

Although intrasire variation among ewes was detectable (P < .001), repeatability was lower than heritability. The resulting repeatability estimate is, however, comparable to values reported elsewhere (Rendel, 1956; Shelton and Menzies; Notter, 1981).

DFL and DBL. Mean squares, their expected values and variance components are listed for DFL and DBL in table 15. For both traits, sire differences were detected (DFL: P < .05; DBL: P < .001). Estimates of h^2 were relatively consistent between REML and least-squares. Since early sexual development may indicate increased fertility in ewes (Drymundsson, 1973) and since the h^2 of DFL exceeds that of first exposure fertility, indirect selection for fertility through DFL may result in more rapid genetic gain.

Among the reproductive traits considered, days between

first and second lambing appears most heritable. Lewis et al. (1990b) proposed using this measure as an alternative to fertility in accelerated lambing systems since it quantifies the frequency of lambing without being season specific. When chronically infertile ewes are ignored (a reasonable restriction since such ewes should always be culled) this measures appears useful in evaluating aseasonality in this accelerated program. The STAR system approximates a continuous lambing program since the time span between the end and start of lambing seasons is only about 40 d. Thus DBL has a fairly continuous, unimodal distribution. In other accelerated lambing programs, such as those involving three lambings per 2 yr, lambing periods are separated by more days and DBL may cluster into non-overlapping groups. DBL may thus be less useful in defining aseasonality in less intensive accelerated programs and its application to such systems requires further study. Modest intrasire ewe variation was found ($P < .05$) and the repeatability of DBL was considerable higher than that for fertility (.079 vs .016). In combination, DFL and DBL appear to provide a more versatile metric measure of aseasonality than does fertility at a given exposure.

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TABLE 13. ANALYSIS OF VARIANCE (ANOVA) AND REML FOR FERTILITY

Item	Effect	First exposure	First post-lambing exposure	All exposures
df	Sire	27	32	44
	Ewe(sire)			956
	Error	682	763	1,789
ANOVA				
MS^a	Sire	.5668	.8334**	.9239***
	Ewe(sire)			.4700
	Error	.4730	.4278	.4914
K value^a	Sire	15.1319(k)	18.9130(k)	3.2747(k_2)
				55.3174(k_3)
	Ewe(sire)			2.7666(k_1)
Var com^b	Sire	.0062	.0214	.0078
	Ewe(sire)			-.0077
h^2		.052 ± .066	.191 ± .088	.063 ± .033
t^c				.016
REML				
Var com^b	Sire	.0017 ± .0121	.0226 ± .0157	
	Error	.4757 ± .0262	.4289 ± .0247	
h^2		.014 ± .101	.200 ± .132	

[a] Mean squares. Expected values for mean squares were $\sigma_e^2 + k\sigma_S^2$ (for sire) or $\sigma_e^2 + k_2\sigma_I^2 + k_3\sigma_S^2$ (for sire) and $\sigma_e^2 + k_1\sigma_I^2$ (for ewe within sire).

[b] Variance components.

[c] Negative variances were assumed zero for repeatability estimation.

**P < .01.

***P < .001.

TABLE 14. ANALYSIS OF VARIANCE (ANOVA) AND REML FOR PROLIFICACY

Item	Effect	First lambing prolificacy	Second lambing prolificacy	All prolificacies
df	Sire	27	35	50
	Ewe(sire)			1,019
	Error	674	732	1,925
ANOVA				
MS[a]	Sire	.3872**	.4367**	.7071***
	Ewe(sire)			.2980***
	Error	.3164	.2463	.2517
K value[a]	Sire	20.0288(k)	17.6078(k)	3.1588(k_2)
				53.7607(k_3)
	Ewe(sire)			2.7832(k_1)
Var com[b]	Sire	.0098	.0108	.0166
	Ewe(sire)			.0075
h^2		.194 ± .091	.168 ± .082	.109 ± .042
t^c				.087
REML				
Var com[b]	Sire	.0079 ± .0075	.0136 ± .0093	
	Error	.1927 ± .0112	.2461 ± .0141	
h^2		.158 ± .144	.210 ± .137	

[a]Mean squares. Expected values for mean squares were $\sigma_e^2 + k\sigma_S^2$ (for sire) or $\sigma_e^2 + k_2\sigma_I^2 + k_3\sigma_S^2$ (for sire) and $\sigma_e^2 + k_1\sigma_I^2$ (for ewe within sire).

[b]Variance components.

[c]Negative variances were assumed zero for repeatability estimation.

**P < .01.

***P < .001.

TABLE 15. ANALYSIS OF VARIANCE (ANOVA) AND REML FOR DFL AND DBL

Item	Effect	DFL	DBL for first to second lambing	All DBL
df	Sire	27	31	36
	Ewe(sire)			679
	Error	674	651	1,132
ANOVA				
MS^a	Sire	26,550*	7,910***	8,511***
	Ewe(sire)			4,167*
	Error	16,439	3,746	3,612
K value[a]	Sire	14.9069(k)	17.8129(k)	3.2101(k_2)
				45.3585(k_3)
	Ewe(sire)			2.5500(k_1)
Var com[b]	Sire	678	234	217
	Ewe(sire)			93
h^2			.158 ± .086	.235 ± .100	.094 ± .051
t^c					.079
REML				
Var com[b]	Sire	986 ± 949	172 ± 133	
	Error	16,425 ± 910	3,803 ± 229	
h^2			.226 ± .206	.173 ± .129	

[a]Mean squares. Expected values for mean squares were σ_e^2 + $k\sigma_S^2$ (for sire) or $\sigma_e^2 + k_2\sigma_I^2 + k_3\sigma_S^2$ (for sire) and $\sigma_e^2 + k_1\sigma_I^2$ (for ewe within sire).

[b]Variance components.

[c]Negative variances were assumed zero for repeatability estimation.

*P < .05.

***P < .001.

Figure 7. Liability scale transformation with threshold at .7458 σ for STAR-born ewes first lambing in January (S1) and with subsequent exposure in March (S2) at interval 1. Of ewes exposed, 22.8% were expected to become pregnant from this exposure. T_{TP} = threshold defined by transition probability (TP) and q_{TP} = expected probability of fertile exposure from TP.
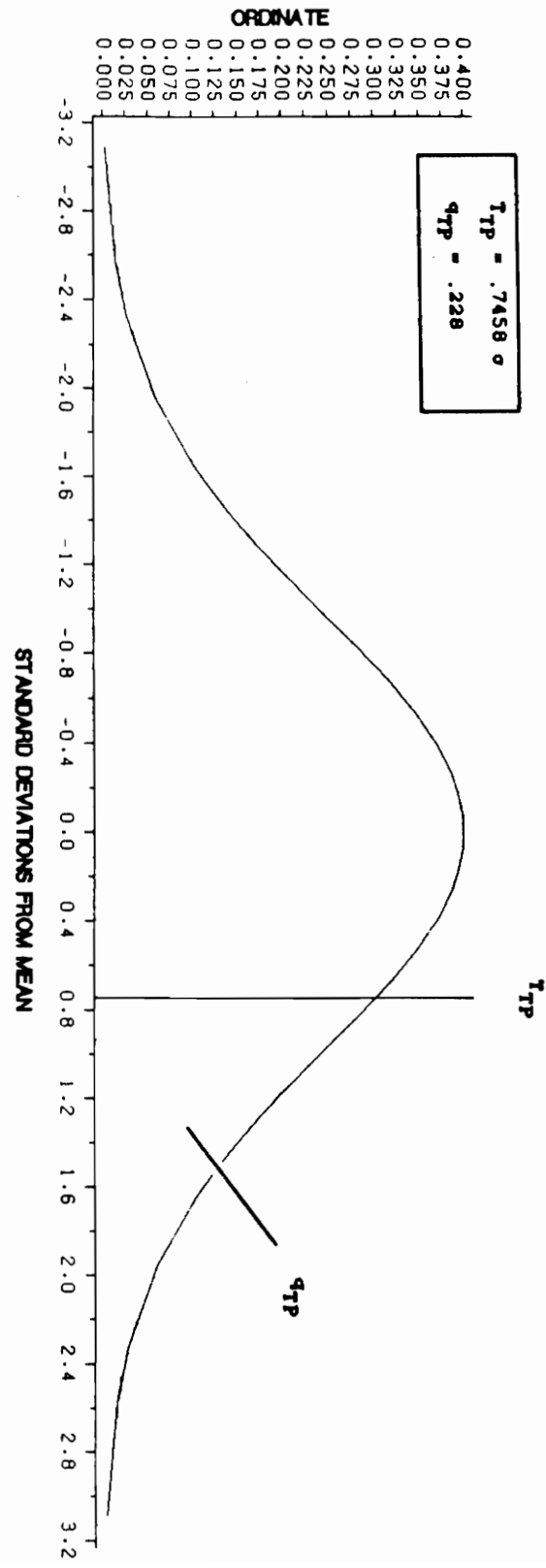
Figure 8. Liability scale transformation of observed mean fertility (38.0%) for all ewes exposed in March (S2), 1986 and thus lambing in August (S4) 1986 and for expected fertility of 24.4% in S2. These corresponds with thresholds at .3047 σ and .6554 σ, respectively. Year adjustment was calculated as the deviation between these thresholds (-.3507 σ). T_O = threshold defined by observed overall fertility for year-season. T_E = threshold defined by expected mean fertility for the season given the distribution of ewes present at that season.
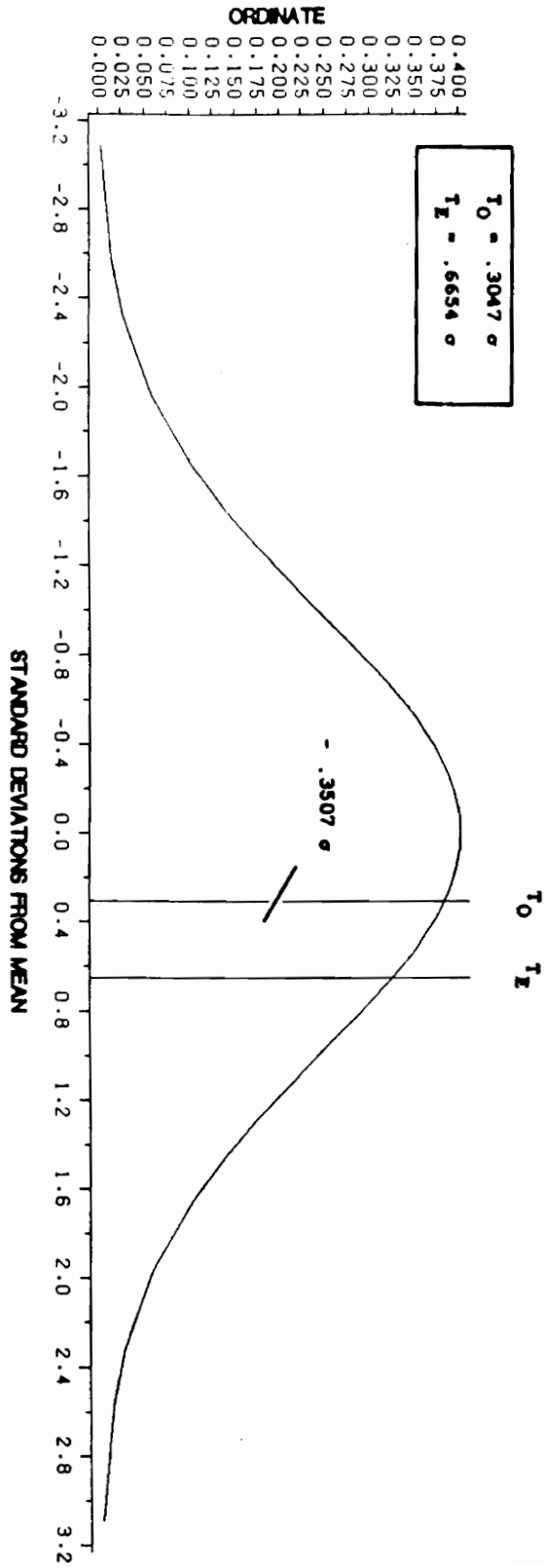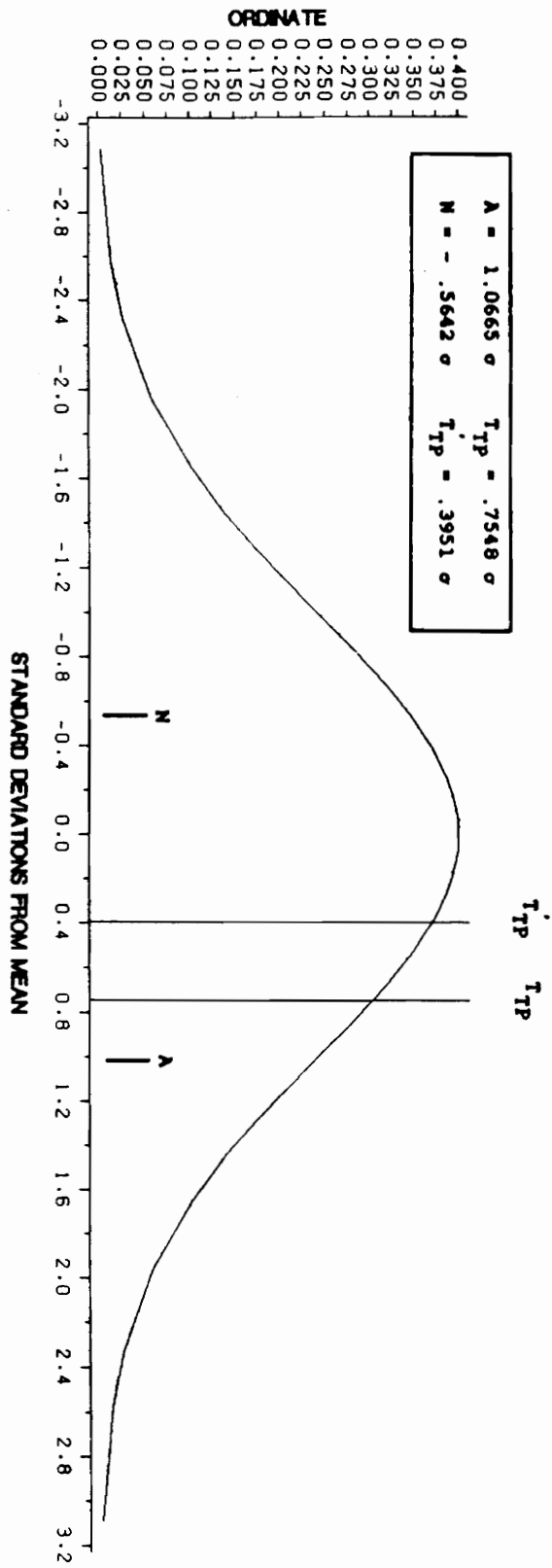
Figure 9. Unadjusted (.7458 σ) and adjusted (.3951 σ) thresholds for STAR-born ewes first lambing in January (S1), 1986 with subsequent exposure in March (S2) at an interval of 1. A and N are the mean phenotypic value for ewes that did and did not lamb. respectively, T_{TP} = threshold defined by transition probability (TP), and T_{TP}= threshold adjusted for year effects.

Vita

My date and place of birth were November 11, 1958 and Inglewood, California, respectively. My parents are Alvin Paul and Elaine Lewis. I earned a Bachelor of Science in Animal Science from the University of California, Davis in June, 1981. I completed a Master of Science in Animal Breeding at Texas A&M University in August, 1986. I was married to Margaret Louanna Perkins on December 16, 1989.

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