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Contents:

Opportunities to Reduce Seasonality of Breeding in Sheep by Selection

D. R. Notter[1]

Introduction

Seasonal reproduction is a serious problem for the sheep industry, reducing effectiveness of accelerated lambing programs, restricting flexibility to integrate lambing into other farm activities, and limiting access to favorable seasonal markets. Environmental or hormonal stimulation of reproduction requires increased investment in feed, labor, and (or) facilities, increases cost of production, often requires access to products that are not readily available or not approved for use in sheep, and may not be feasible in extensive or semi-extensive production systems. However, less intensive and less costly management interventions are available to improve reproduction; chief among these is use of the ram effect (Oldham and Fisher, 1992). In addition, substantial evidence exists to document genetic differences in seasonality of breeding, leading to opportunities to reduce seasonality by selection.

This review will address potential for genetic improvement of reproduction in sheep in both annual autumn and accelerated lambing systems. Satisfactory reproductive performance in both systems is mainly limited by the need to lengthen the breeding season to encompass spring and summer matings. In annual lambing, a shift in the annual pattern of reproductive behavior may be sufficient to meet the needs of the program, and ram effect is a useful tool for induction of estrus. In contrast, accelerated lambing systems place a premium on rapid rebreeding which is not required in annual lambing. Accelerated systems thus generally require more careful timing of ram effect and greater genetic sensitivity of ewes to ram introduction.

Selection to reduce seasonality of breeding involves application of the principles well-established. Selection among existing breeds is used to establish a flock with desirable initial characteristics. A breeding program is then designed to appropriately utilize complementary breed effects and hybrid vigor. And finally, selection within the flock is implemented to generate genetic improvement in economically important traits.

Seasonal Patterns of Reproduction in Sheep

A typical pattern of seasonal variation in occurrence of estrus for temperate sheep breeds is shown in Figure 1, derived from results summarized by Notter (1992), with dramatically reduced fertility in spring and summer. However, the dates of onset and cessation of anestrus vary widely with breed, latitude, and management. For some breeds and at some locations, the seasonal anestrus may not be absolute, with some ewes in estrus during each month of the year (Wiggins et al., 1970; Hall et al., 1986). However, even in relatively nonseasonal breeds, most ewes appear to become anestrus at some time during the year. Documented continuous cyclicity is rare. Hall et al. (1986) reported that only four of 73 Dorset ewes in a New Zealand experiment cycled continuously for a period of 15 mo. Wiggins et al. (1970) reported that two of 23 Rambouillet ewes in an Alabama flock cycled continuously for 4 yr. More recently, Vincent et al. (2000) documented continuous occurrence of estrus during spring and summer in a high proportion of ewes from a population selected for out-of-season breeding.

The duration of seasonal anestrus in the ewe may be modified by introduction of males to the flock. In anestrous ewes that have been isolated from males, introduction of rams commonly induces ovulation in a proportion of the ewes, whereas ewes that remain isolated from males remain anestrus. Likewise, ewes that have been in continuous contact with rams during anestrus take longer to begin cycling than ewes that were separated from, and then reintroduced to, rams, although the introduction of unfamiliar rams may induce some ewes to cycle.

Variation in number of lambs born is also commonly observed among ewes lambing in different seasons. Ovulation rate is commonly reduced in ewes cycling in spring and summer (Quirke et al., 1988), and embryonic mortality may be increased, especially if ewes are exposed to high summer temperatures during gestation. An example of seasonal variation in number of lambs born per ewe lambing in different ewe types is reproduced in Figure 2 (Notter and Copenhaver, 1980). In general, the average number of lambs born per ewe lambing is reduced by one third to one half of a lamb in adult ewes lambing in autumn. Heat stress during gestation may also influence lamb birth weights and perinatal mortality (Shelton, 1964; Shelton and Huston, 1968). Al-Shorepy and Notter (1998) reported that autumn-born lambs in

1 Dept. of Animal and Poultry Sciences, Virginia Polytechnic Institute and State University, Blacksburg. Phone (540) 231-5135. Fax (540) 231-3010. Email drnotter@vt.edu.

Virginia averaged .6 kg less at birth than spring-born lambs, with associated increases in lamb mortality.

Environmental and Neuroendocrine Control of Seasonal Breeding

Changes in reproductive status in the sheep are associated with changes in day length. The response of the ewe to changing light conditions is mediated by the hormone melatonin from the pineal gland. Cells in the pineal gland possess neuroendocrine connections to the optic nerve and respond to light signals from the eye. In darkness, the pineal typically produces melatonin at mean levels of 100 to 300 ng/ml of circulating blood plasma. During the day, or under artificial lighting, circulating melatonin levels drop precipitously, with mean levels generally below 30 ng/ml. Circulating melatonin levels thus reflect external light conditions. Seasonal changes in the daily pattern of circulating melatonin, as opposed to absolute circulating levels of the hormone, are the main factor controlling seasonal changes in reproduction.

Expression of seasonal reproduction requires cyclic changes in day length. Under controlled lighting, the seasonal reproductive pattern can be accelerated by increasing the rate of change in day length, and two complete cycles of reproductive activity/inactivity can be induced in a 12-mo period by doubling the daily rate of change in day length. However, Robinson and Karsch (1984) and Robinson et al. (1985) have shown that exposure to a constant day length (either long or short) cannot maintain the ewe in a constant reproductive state. Highly seasonal Suffolk ewes maintained under constant light conditions for more than 12 to 13 wk following either the winter or summer solstice exhibited spontaneous changes in reproductive state that were independent of both day length and circulating melatonin levels. This response indicates that there is an internal mechanism in the ewe that is capable of producing cyclical changes in reproductive status. Changes in day length can interact with this internal cycle to modify, but not eliminate, seasonal reproduction. In practical breeding programs, manipulation of reproduction by controlled lighting thus requires modification of the pattern of change in day length rather than simple imposition of a constant, stimulatory photoperiod.

The ram effect is controlled by a pheromone produced by the male, which explains why expression of ram effect requires a period of isolation from males (to prevent ewes from becoming refractory to the pheromone), why males may differ in ability to induce ram effect, and why new rams may be able to induce estrus (differences in chemical structure or level of production of pheromone). The endocrine events that follow ram introduction are well-known (Martin et al., 1986). Ewes that respond to ram effect generally have an increase in pulsatile release of luteinizing hormone (LH) from the anterior pituitary gland within a few minutes of ram exposure. This pattern of LH release causes ovulation, usually within 1 to 2 d of ram introduction. The first ovulation is generally not accompanied by estrus; instead, the first estrus is anticipated to occur at the second ovulation, 18 to 19 d after ram introduction. Also, in some ewes, estrus is further delayed by formation of an incompetent corpus luteum (CL) at first ovulation. In these ewes, the first CL regresses prematurely, 5 to 6 d after ovulation. A second ovulation may then occur 6 to 8 d after ram introduction but is again not usually associated with estrus. If a normal CL is formed after the second ovulation, a third ovulation, now accompanied by the first estrus, is anticipated about 24 d after ram introduction. Classical expression of ram effect in highly responsive Australian Merino ewes thus involves two periods of estrus activity at about 19 and 24 d after ram introduction (Oldham and Fisher, 1992). However, both Nugent et al. (1988) and Cushwa et al. (1992) observed less tightly synchronized responses to ram introduction in U.S. breeds.

Ram effect is most useful in advancing the onset of the breeding season by 4 to 6 wk and is perhaps the most effective management tool available for accomplishing this objective. Some ewes also respond to ram effect in early to mid-anestrus, but fewer ewes generally respond, and the response is less reliable, in part because some ewes ovulate only once (without estrus) and then return to anestrus. Figure 3 displays anticipated responses to ram introduction at different seasons (derived from concepts and data presented by Martin et al., 1996, and Oldham and Fisher, 1992).

Breed Effects and Heterosis

Breed differences in duration and timing of the breeding season are readily demonstrated, beginning with Hafez (1952). Among North American breeds, Dorsets are generally considered to be less seasonal than other breeds. However, Rambouillet and Finnsheep also have considerable potential for out-of-season breeding, and crosses involving Dorset, Rambouillet, and (or) Finnsheep have commonly been superior to other breeds and crosses (Notter and Copenhaver, 1980; Fogarty et al., 1984). Finnsheep may continue cycling longer in spring, but also initiate cycles later in fall, than Rambouillet or Merino ewes (Quirke et al., 1988; Wheeler and Land, 1977). Hulet et al. (1984) demonstrated that Polypay ewes, derived from crosses among Dorset, Rambouillet, Targhee, and Finnsheep, had better out-of-season fertility than several of the component breeds and crosses. Conversely, breeds such as the Suffolk, Hampshire, and Columbia generally are poor out-of-season breeders (Dufour, 1974; Jeffcoate et al., 1984).

Breed differences in responsiveness of ewes to ram effect may contribute to differences in out-of-season breeding. Ewes of Merino type (including American Rambouillet) and most Mediterranean breeds are highly sensitive to ram effect, especially in summer. Nugent et al. (1988) reported that Dorset ewes responded to ram effect in both May and June, whereas Hampshire ewes responded in June but were much less responsive than Dorsets in May. Breed differences in the ability of males to elicit ram effect have been reported. Dorset rams were more effective than Romney rams in inducing estrus in New Zealand Romney ewes (Tervit and Peterson, 1978; Knight et al., 1980). Nugent and Notter (1990) also reported that ewes exposed to Dorset rams lambed earlier than ewes exposed to Suffolk rams. Breed differences in performance in accelerated lambing have also been reported. Notter and Copenhaver (1980) reported that with three lambing opportunities every 2 yr, Finnsheep x Rambouillet ewes lambed more frequently than 25%-Finnsheep, 75%-Rambouillet ewes; Suffolk x Rambouillet ewes lambed least frequently.

Few studies have measured heterosis for traits associated with seasonal breeding. Dufour (1974) reported that ewes of 50% Dorset, 25% Leicester, and 25% Suffolk breeding had a longer breeding season than any of the component breeds, but some selection may have occurred within the crossbreds. Quirke et al. (1988) reported that the breeding season of crosses between Dorset, Rambouillet, and Finnsheep averaged only 9 d longer than that of the purebreds, and Clarke (1985) observed that fertility of Finnsheep x Dorset ewes in April and May was slightly inferior to that of the purebreds. In the male, Whiteman (1976) reported that Suffolk x Hampshire rams settled more ewes than rams of the parent breeds in summer, but not in autumn.

There is perhaps little reason to anticipate heterosis for duration of the breeding season in the sheep. In each breed, natural selection is anticipated to have resulted in establishment of a pattern of breeding behavior appropriate to the evolutionary history of that breed. Genetic mechanisms which control the breeding season are not understood, so strong predictions cannot be made about length and timing of breeding in crossbreds.

Development of Breeding Programs

Breeding programs for out-of-season or accelerated lambing generally involve some sort of terminal sire crossbreeding program. Breeds with the greatest capacity for out-of-season breeding are generally moderate in size and growth rate and relatively early maturing. Increases in lamb value can be attained by crossing such ewes to rams of larger later-maturing breeds to increase growth rate and leanness.

The typical terminal sire breeds (e.g., the Suffolk, Hampshire, Columbia, and Texel) are generally poor out-of-season breeders and not optimal as ewe breeds in out-of-season or accelerated lambing. However, rams of even these seasonal breeds usually do not become completely sexually inactive during spring and summer and, if carefully managed, can often be used in crossbreeding throughout the year. Certainly, when rams of seasonal breeds are used, breeding soundness and serving capacity tests should be administered, ram:ewe ratios should be increased, rams should be equipped with marking harness to monitor mating, and multiple-sire breeding pastures should be favored.

An important decision in designing breeding programs will be whether to use breeding rams of less seasonal breeds such as the Dorset instead of rams of larger, but also usually more seasonal, meat breeds. Use of rams of less seasonal breeds may enhance fertility but can reduce lamb growth rates and carcass value. This decision likely will be influenced by the prevalence of other factors that may potentiate unfavorable light conditions, including high temperature, high humidity, little access to shade, and difficult, extensive grazing conditions. As the number of seasonal stress factors goes up, the potential value of less seasonal sire breeds also increases, as does the need for more intensive management of breeding rams.

Selection

Selection to reduce seasonality in a fixed annual season or to improve overall performance in accelerated lambing presents unique challenges relative to other genetic improvement programs. While principles of genetic improvement are common to all traits, their application is more difficult for complex reproductive traits.

Annual, out-of-season lambing.
Genetic improvement of fertility in spring and summer requires that animals be allowed to express genetic differences in fertility, whereas profitable sheep production dictates that every effort be made to maximize reproductive performance. Thus, breeding programs directed at genetic improvement usually involve two phases: 1) a challenge phase, in which animals are given the opportunity to express genetic differences, and 2) a clean-up phase in which animals that do not become pregnant in the challenge phase are given a second opportunity to conceive under either more favorable environmental conditions or more intensive reproductive management.

The objective of the selection is to improve performance during the challenge phase to a level that will allow clean-up matings to become unnecessary. Further, the clean-up phase must be designed so that it will not have a negative impact on ewe performance in next year's challenge phase. Figure 4 shows a scheme for a primary spring breeding followed by late-summer clean-up matings. In addition, the primary spring mating is structured to allow discrimination between ewes that are naturally cycling at the start of mating and those that are induced to cycle by ram effect. Early weaning (at 45 to 60 d) of lambs from clean-up matings provides ewes with adequate time to recover from lactation and express their rebreeding potential at the next spring mating. Dzabirski and Notter (1989) found that Dorset ewes lambing in January were less likely than ewes that lambed in October to cycle spontaneously in the following April, but did not differ from ewes that had lambed in October in mean fertility or lambing date.

This design was used at Virginia to develop animals with increased fertility in May and June (Al-Shorepy and Notter, 1996, 1997; Notter et al., 1998). In the early years of the project, when mean fertility of adult ewes averaged about .5, all ewes were exposed to several vasectomized rams in a single group for 2 wk before the start of the May breeding. As mean performance improved, use of teaser rams was eventually discontinued and ewes were isolated from rams before breeding. Under this protocol, shown in Figure 4, ewes that lamb in the first 2 wk of the lambing season were assumed to have been cycling at the time of ram introduction and were favored in selection. Later-born lambs were more likely to have been born to ewes that responded to ram effect and were discriminated against, particularly in choosing male replacements.

The schedule shown in Figure 4 is preferable to leaving rams with ewes until the start of the next natural breeding season. Ewes can be isolated from rams during July and thereby respond to ram effect when rams are reintroduced in August. Continuous ram exposure can cause ewes to become desensitized to ram effect, reducing fertility in clean-up matings.

An alternative plan for the clean-up phase (Figure 4) would be to use some sort of pharmacological treatment on ewes at the end of the challenge phase. Such a strategy must be designed with care to avoid negative effects on ewes that become pregnant early in the challenge phase, but treatments involving melangesterol acetate, controlled lighting, or melatonin supplementation would potentially be useful. This sort of intensive treatment during the clean-up phase will likely be required if ewes are to be bred before August. Results in the Virginia Tech selection project suggest that most ewes that conceive during the challenge phase do so within the first 30 d of breeding (D. R. Notter, unpublished); ewes that are not cycling spontaneously and do not respond to ram effect in May appear unlikely to begin cycling in June. In that experiment, treatments to stimulate clean-up matings could have been imposed by June 1 without compromising selection.

A particular concern in annual out-of-season lambing programs is how to best introduce replacement ewe lambs to the system. Fertility of autumn-born ewe lambs exposed in spring to lamb for the first time at 12 mo of age is almost always poor, yet these are the animals that are expected to be genetically superior as adults in out-of-season breeding. Notter et al. (1998) reported that selection increased fertility of adult ewes in May to over 80% but that fertility of 7-mo-old selected ewe lambs averaged only 15% and had not responded to selection. Under the scheme shown in Figure 4, most ewe lambs will lamb for the first time in January at 15 mo of age. Care is required in managing these animals to maximize their probability of rebreeding. They should be separated from adult ewes and weaning of lambs should occur as early as practical.

Matings during the challenge phase usually involve single-sire breeding pastures to provide pedigree information used in genetic evaluation. Careful evaluation of ram breeding status is critical to avoid infertile rams with associated loss in information about ewe genetic merit. At Virginia Tech, 7-mo-old fall-born ram lambs did not show the same problems in breeding that were observed in ewe lambs. In most years, a few ram lambs were sexually inactive based on serving capacity tests, but among males that passed serving capacity and breeding soundness exams, fertility did not differ between ram lambs and older males, albeit at low ram:ewe ratios of about 1:15.

Direct selection in males for reduced seasonality, or for other reproductive traits that may be associated with seasonality, is also possible. Sheep breeds differ in their ability to elicit the ram effect, and individual animal differences likely also exist. However, very few studies have documented effects of selection to improve male fertility in sheep. Direct selection of males for fertility in spring and summer matings is generally not feasible because relatively few males are actually used in breeding. Instead, some sort of screening procedure such as the serving capacity tests described by Perkins et al. (1992) must be used. Selection of males could directly improve breeding capacity of the male in spring and summer (Perkins and Fitzgerald, 1994) or could result in correlated changes in female traits associated with seasonality. Thus when Haley et al. (1990) selected for rapid early testicular growth relative to body size in males, daughters of selected males were observed to have an earlier date of onset of the breeding season.

Requirements for data recording in annual lambing programs are relatively straightforward. Breeding records must be maintained, along with information on which ewes lamb and their date of lambing to allow discrimination among ewes that lamb to matings during the challenge phase, the clean-up phase, or not at all. Records on ewe disposals or deaths are required to account for animals removed from the flock between breeding and lambing. The number of lambs born should be recorded; ovulation rates are normally reduced in spring matings, and animals that produce multiple births may be less seasonal than those that produce singles (Al-Shorepy and Notter, 1996). Records of birth weights are recommended; low birth weights and associated increases in lamb mortality in autumn lambs can occur in some environments and have a significant maternal genetic component (Al-Shorepy and Notter, 1998). Other characteristics (body weights, wool characteristics, etc.) should be recorded as needed to support genetic improvement in other economically important traits.

Most sheep recording programs permit, but do not require, detailed recording of mating and ewe disposal dates. The U.S. National Sheep Improvement Program (NSIP) encourages breeders to report complete mating and ewe disposal information, but many breeders focus on lambing rather than mating records when reporting data. Mating information on ewes that do not lamb is often missing.

Genetic analysis of reproductive traits in general and fertility records in particular presents a number of unique challenges. Most reproductive traits are lowly heritable, commonly 10% or less (Fogarty, 1995), but have reasonably high levels of variation which can support annual rates of improvement of 1 to 2% per year. Records of reproductive performance usually fall into one of a few distinct categories (e.g., pregnant or not; produced one, two, or three lambs; lambed during the challenge phase, clean-up phase, or not at all) rather than producing a continuous distribution of values characteristic of traits such as weaning weight or fiber diameter.

Categorical expression of performance (Figure 5) complicates discrimination among candidates for selection. The model commonly used for expression of categorical traits assumes that animals in the flock possess an underlying continuous distribution of lambing potentials. This underlying distribution of potentials is translated to the observed performance categories by invoking a series of thresholds. In Figure 5a, the 5% of ewes with the highest lambing potential have triplets, the 40% with the lowest potential have singles, and the remaining 55% have twins. The location of the thresholds is influenced by nongenetic effects such as ewe age. Thus the ewe lambs shown in Figure 5b have a similar distribution of lambing potentials to the adult ewes in Figure 5a, but a different set of thresholds, leading to different frequencies of multiple births.

In Figure 5, each category contains animals with substantial differences in underlying lambing potential. Only rarely will the number of replacements required correspond exactly to the number of individuals found in the most desired class(es). In Figure 5, selection of replacement males from those born as triplets would come close to maximizing intensity of selection for number born. But in choosing replacement females, some twin lambs will be kept while others will be rejected.

Comparison of animals in different age groups is more difficult for categorical traits than for continuously distributed traits. A ewe lamb with twins is, on average, better in terms of underlying reproductive potential than an adult ewe with twins, but the two groups overlap in term of underlying reproductive potential. Optimal solution to the problem of predicting genetic merit for these reproductive traits involves:

1. Application of relatively sophisticated statistical methodology to directly account for the categorical expression of most reproductive traits and to properly weight records made by ewes of different ages or evaluated under different conditions. These methods are not widely accessible, although they have been applied to genetic evaluation of calving difficulty in beef and dairy cattle.
2. Use of repeated records to increase the number of categories and thereby make it easier to discriminate among candidates for selection. Thus, if the data represented in Figure 5a were collected over 2 yr, there would be six outcome groups (single-single, single-twin, single-triplet, twin-twin, twin-triplet, and triplet-triplet) making discrimination easier, but still leaving the problem of deciding if a twin-twin or a triplet-single pattern is more desirable. [Note that in Figure 5a, the triplet-single pattern is slightly more desirable based on mean value on the underlying scale.]
3. Use of records of relatives to augment individual records and thereby make the distribution of records more continuous. This strategy is currently the basis for genetic evaluation in most programs, including NSIP, and also accounts for animals with different numbers of records.

Results presented by Notter et al. (1998) suggest that genetic improvement in spring fertility can be achieved without use of explicit categorical methodology, although use of these methods should accelerate genetic improvement. Vincent et al. (2000) also demonstrated that this selection was successful in lengthening the breeding season. Genetic evaluations for out-of-season fertility in a single annual breeding season would thus be relatively easy to incorporate into existing programs such as NSIP.

Accelerated lambing.
Genetic improvement of reproductive performance in accelerated lambing involves most of the issues discussed above for annual, out-of-season lambing as well as an array of additional issues involving the need for ewes to rebreed quickly after weaning lambs. Breeding seasons under accelerated lambing are usually short, with animals that do not become pregnant advancing to the next breeding season within a few weeks while animals that conceive go on to lamb and then return to breeding at a later date. Animals that do not breed in spring or summer accumulate, with most eventually conceiving at a late-summer or autumn breeding that effectively represents the "clean-up" matings of Figure 4.

Opportunities to use ram effect in accelerated systems are limited. In the STAR system (Figure 6; Hogue et al., 1980), ewes go into breeding 7 d after weaning their lambs and breeding seasons are only 30 d long, so ram effect must be generated by breeding rams. Because ewes responding to ram effect usually conceive 19 to 20 or 25 d after ram introduction, early lambing in accelerated systems requires that ewes be cycling at the start of breeding. Notter (1989) demonstrated that introduction of vasectomized rams before weaning did not advance the date of first estrus. Use of vasectomized rams of a lowly seasonal, high-libido breed such as the Finnsheep, Romanov, or Barbados Blackbelly in the breeding pastures might merit study. Care would be required to avoid dominance of the vasectomized ram over the intact breeding ram.

Selection and management of replacement females is particularly challenging in accelerated lambing. Ewe lambs born in autumn are anticipated to be genetically superior, but usually have very poor fertility in the next spring, and are unlikely to lamb at 12 mo of age. In the system of three lambings every 2 yr shown in Figure 7, autumn-born ewe lambs are unlikely to conceive until August at 11 mo of age. In contrast, most lambs born in January or April should be able to mate at 7 mo and lamb at 12 mo of age but, on average, are not expected to be genetically superior for out-of-season breeding. A solution to this conundrum is to use prior lambing records of the dams to identify superior spring-born lambs. In Figure 7, ewes that lamb in September are anticipated to next lamb in April. April-born daughters of these ewes can be retained and allowed to lamb for the first time the next April, and are then anticipated to be capable of good performance in later, out-of-season matings.

Recording of performance in accelerated lambing is a challenge. Accurate records of matings, lambings, and ewe deaths or sales are required to ensure that both successful and unsuccessful matings are properly recorded. Descriptions of accelerated programs such as those in Figures 6 and 7 generally indicate that all nonpregnant ewes are to be placed with rams at each mating season. However, this recommendation is not always followed; producers commonly modify systems to meet specific management and marketing goals. Thus in a system like STAR, ewes that lamb very late in one season may be judged to be unable to breed in the next available season and not exposed until a later season. Breeding of ewes may also at times be deferred for a season to even out numbers of lambs produced at different times. These decisions can cause ewes to fail to lamb on schedule, and unless mating records are scrupulously maintained, can result in ewes being improperly penalized for not lambing. Use of data from accelerated lambing in NSIP will likely require records of the starting and ending date of each mating period, of the ewes placed with rams in each period, and of all subsequent lambings.

Accurate ewe disposal records are also needed to ensure that ewes that die or are sold after breeding but before lambing are not entered into the data as open ewes. While such errors are not important to evaluation of the ewe herself, under most genetic evaluation systems, records of a ewe also impact the genetic evaluation of her relatives who may still be in the flock.

More factors influence performance in accelerated lambing than in annual lambing, and care must be taken to recognize, and in some cases adjust for, these factors. Since ewes are expected to rebreed shortly after weaning lambs, factors associated with the previous lactation may impact the ewes' condition and (or) physiological state of the start at breeding, thereby influencing subsequent fertility. Many of these factors are themselves under partial genetic control and may be influenced by selection to enhance reproduction. Time of previous lambing has important effects on current fertility. Thus ewes that did not lactate immediately before entry into breeding may be genetically inferior, since they missed at least one previous lambing opportunity, but have had more time to recover from their last lactation, which is expected to make them more likely to cycle and conceive. Even among ewes that are being rebred just after weaning, date of previous lambing may influence subsequent performance. Thus ewes that lamb late in one season are less likely to conceive at their next opportunity. Initial poor performance by such ewes thus places them in a situation that is conducive to repeated poor performance. Procedures to adjust for the non-genetic portion of this relationship, while not compromising genetic information, still need to be developed.

Selection for rapid rebreeding potential may have negative correlated effects on milk production because ewes that give less milk are anticipated to be in better condition at breeding. Similarly, ewes that can produce twins and triplets in autumn may be less seasonal than ewes that produce singles but the additional nursing stimulus of multiple lambs may affect rebreeding and subsequent ovulation rates. Genetic relationships involving these traits have not been determined, but it will be important in accelerated systems to evaluate ewes for the full spectrum of performance traits.

Perhaps the main complication to properly analyzing data from accelerated lambing systems is that the ewes are not maintained as a single contemporary group. Instead, ewes have different breeding patterns over time and these patterns depend on previous performance. After each breeding, the open ewes and the pregnant ewes follow different paths and subsequently end up in different breeding groups. Average genetic merit is thus expected to differ among ewes in different breeding groups. These differences should be accounted for in genetic evaluation but this requires application of relatively sophisticated methodology.

The issues of how to properly collect, adjust, analyze, and report data from accelerated lambing systems have not yet been adequately addressed. Lewis et al. (1998), in an analysis of the Cornell University STAR Dorset flock, reported that age at first lambing and the length of the first two lambing intervals were heritable traits which could be useful in genetic improvement. But lengths of later lambing intervals were not heritable, suggesting that cumulative environmental effects progressively complicated genetic evaluations in older ewes. Incorporation of these traits into NSIP was proposed (Notter, 1998) but has not yet been accomplished. The alternative of imposing a categorical genetic evaluation model to use results of all exposures for each ewe is likewise being considered but would require a substantial development effort.

Molecular Approaches to Reducing Seasonality

Use of molecular techniques to aid in identification of genetically superior individuals is appealing for traits involved in seasonal breeding. Direct selection for these traits is difficult. As noted above, a challenge phase of some sort is required to allow expression of individual differences in performance but, unless carefully managed and coupled with an effective clean-up phase, may reduce overall flock productivity and profitability. In addition, seasonality is difficult to measure in large numbers of males, effectively limiting expression of performance to ewes; low fertility in ewe lambs postpones evaluation of performance to the second and subsequent lambing opportunities; and heritability is low, even under the best of conditions. Under conditions of low heritability, with expression of the trait limited to one sex and to relatively advanced ages, the identification of DNA-based molecular markers would be advantageous, allowing results of DNA testing of animals of both sexes early in life to be used as a preliminary criterion to identify genetically superior individuals. Also, reliance on the challenge phase to identify superior individuals might be reduced, although probably not eliminated.

Two broad options exist for use of molecular information in genetic improvement of seasonality. The first involves direct identification of genes that control seasonal breeding and development of DNA tests to identify favorable variants at these loci. This approach has been taken for the deleterious Spider Lamb condition, and for the Booroola Fecundity gene. Both arise from mutations that can now be identified by DNA tests (Cockett et al., 1999; Wilson et al., 2001). The Invermay fecundity gene in New Zealand Romney sheep (Galloway et al., 2000) increases ovulation rate and results from a mutation on the X chromosome. Recent studies by Pelletier et al. (2000) and Notter et al. 2002 suggest that seasonality may be associated with genetic variation in the melatonin receptor gene.

An alternative strategy may be used when the location of a gene influencing performance is not known. This approach involves use of marker genes, bits of polymorphic DNA which do not themselves influence seasonality but which are known to be associated with genes that do, through proximity to these genes on a chromosome. However, marker genes normally differ among breeds and families within breeds, so reliable use of marker genes requires relatively extensive genotyping of animals in each flock. Marker associations can also be disrupted by recombination and thus must be periodically reassessed. Genetic markers have been identified for the callipyge gene (Berghmans et al., 2000), but the actual mutation has not yet been identified.

The cost of using molecular data in selection is modest, but the cost of locating genes or establishing genetic marker associations is substantial, especially when a gene of major effect is not already known to exist. Large numbers of matings with intensive evaluation of animals for traits of interest are required to identify useful genes or markers. Such investments have been made by some swine and poultry breeding companies but will be more difficult for the smaller, less-organized U.S. sheep industry.

Conclusions

Genetic differences in seasonal breeding patterns clearly are present among and within U.S. sheep breeds. Appropriate choices among ewe breeds and crosses, when coupled with careful management of breeding rams and use of the ram effect, can result in fertility levels of 50 to 70% in most seasons. Selection within breeds can further reduce seasonality but requires carefully designed evaluation programs to accurately identify superior individuals. Collection of data for evaluation of seasonality in industry programs such as NSIP is possible but will require detailed reporting of mating, lambing, and ewe disposal information.

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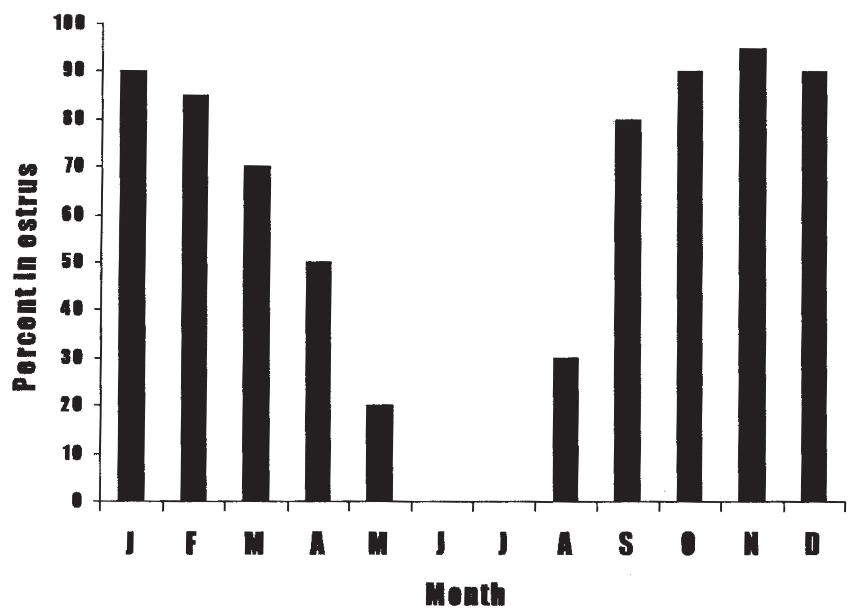

Figure 1. Anticipated proportion of ewes exhibiting estrus in different months (derived from results summarized by Notter, 1992).

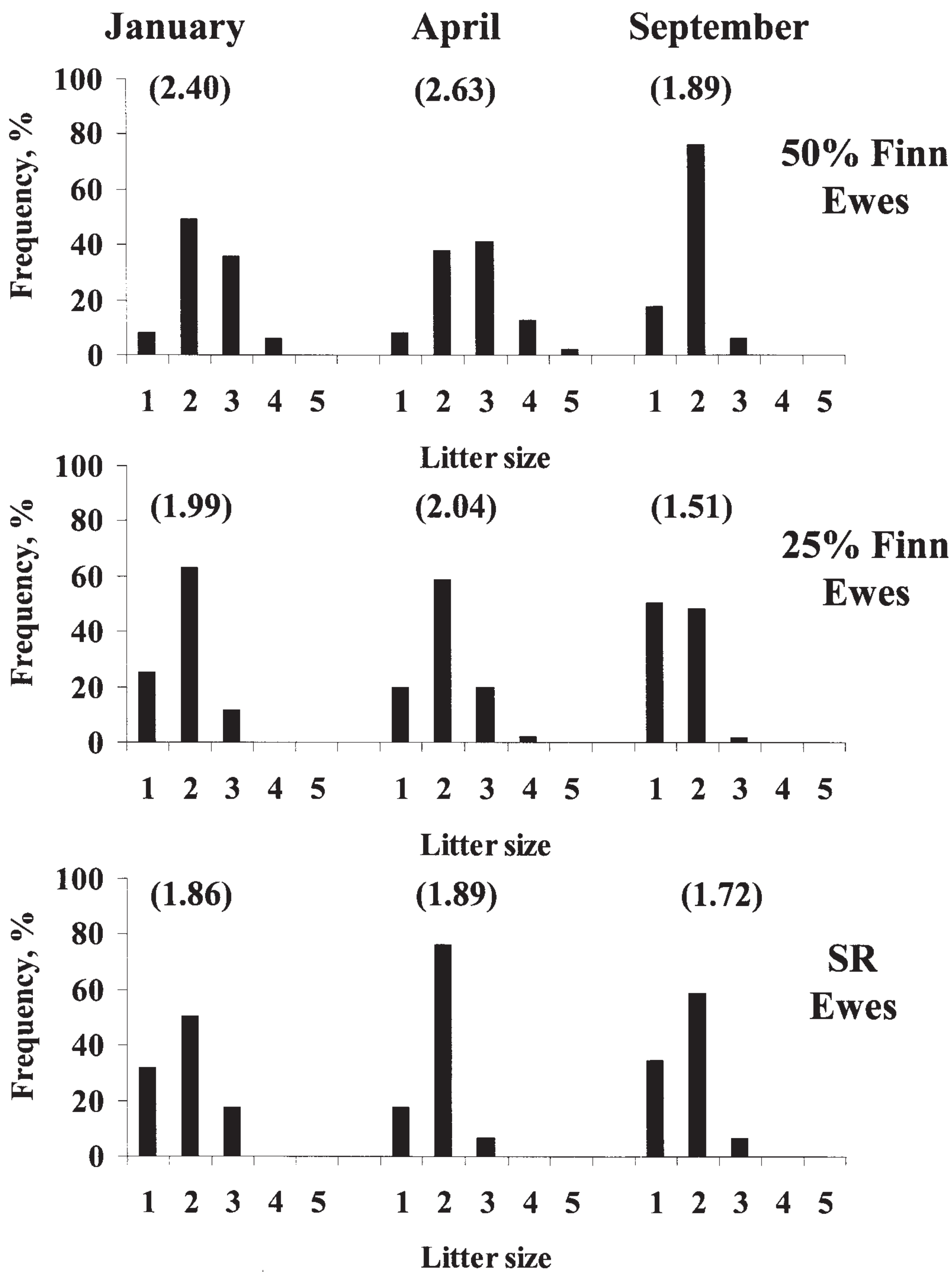

Figure 2. Distribution of litter sizes for 50% Finnsheep, 50% Rambouillet (top); 25% Finnsheep, 75% Rambouillet (center); and 50% Suffolk, 50% Rambouillet (bottom) ewes lambing in January, April, or September (from Notter and Copenhaver, 1980). Mean litter size is shown in parentheses for each season and breed type. ©J. Anim. Sci. 54:1039.

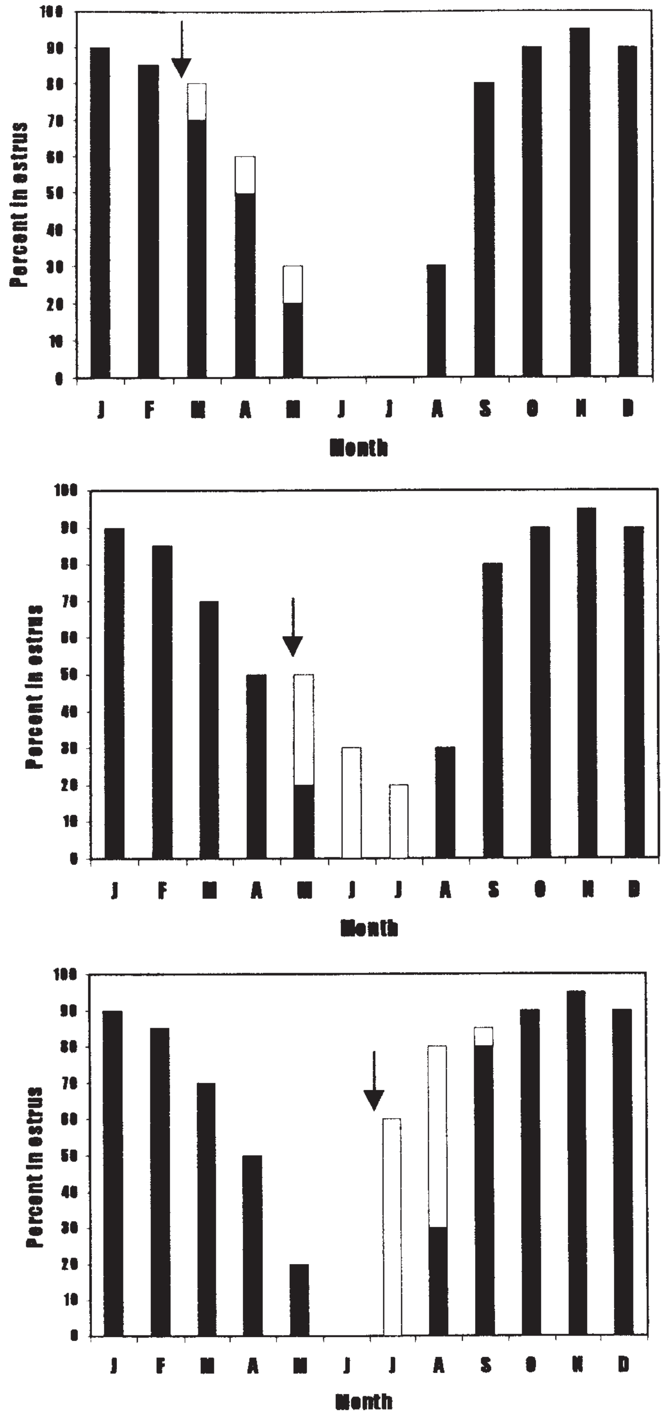

Figure 3. Anticipated effect of ram introduction at different times of the year on occurrence of estrus. Arrows designate the time of ram introduction. Closed bars show the frequency of estrus in ewes continually exposed to rams. Open bars show anticipated frequency of estrus with use of ram effect.

Month	Activity
Jan	
Feb	
Mar	Ram isolation
Apr	Ram isolation
May	Challenge breeding
June	Challenge breeding
July	Ram isolation
Aug	Clean-up breeding
Sept	
Oct	Challenge lambing
Nov	Challenge lambing
Dec	Challenge weaning (Dec. 20)
Jan	Clean-up lambing
Feb	
Mar	Clean-up weaning (Mar. 15) Ram isolation
Apr	Ram isolation
May	Challenge breeding
June	Challenge breeding
July	

or

Mar. 15-April 14	Ram isolation
April 15-30	Teaser rams

detail

Oct. 1-14	Lambs born to ewes that were cycling
Oct. 15-31	Lambs born to ewes induced to cycle by ram effect
Nov. 1-30	Lambs born to 2nd matings or to late responders to ram effect

Figure 4. A breeding schedule for evaluation of seasonality. This program assumes isolation of ewes from rams in March and April but can be modified as shown to incorporate use of teaser rams before breeding. The relationship between lambing date and ewe mating behavior is also shown in detail for ewes that were not teased before the start of breeding.

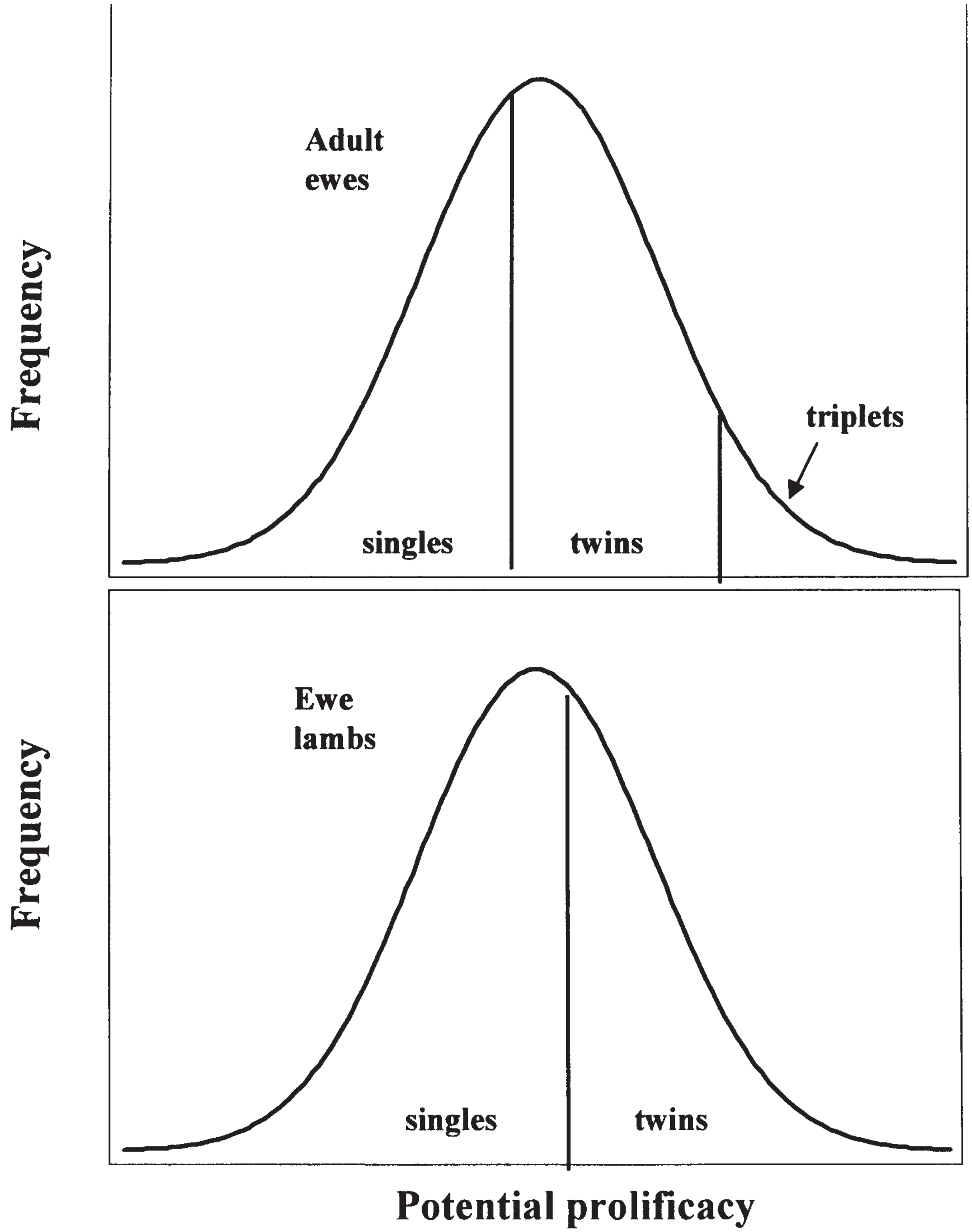

Figure 5. An example of categorical expression of a reproductive trait (litter size). Adult ewes and ewe lambs are assumed to have the same distribution of potential prolificacy on the horizontal axis. Animals that exceed critical levels (thresholds) in underlying potentials produce twins or triplets whereas remaining ewes produce singles. Effects of ewe age on litter size are produced by varying the location of the thresholds.

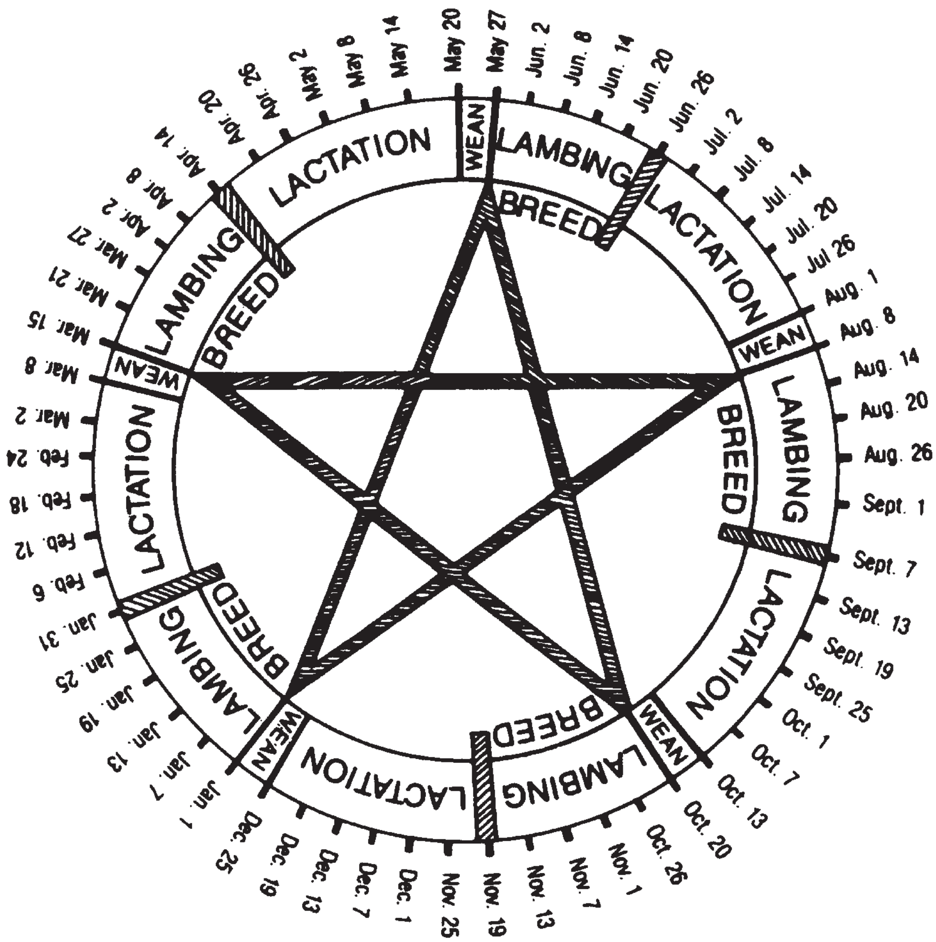

Figure 6. The STAR accelerated lambing system (Hogue et al., 1980). ©Cornell Research Foundation (1984).

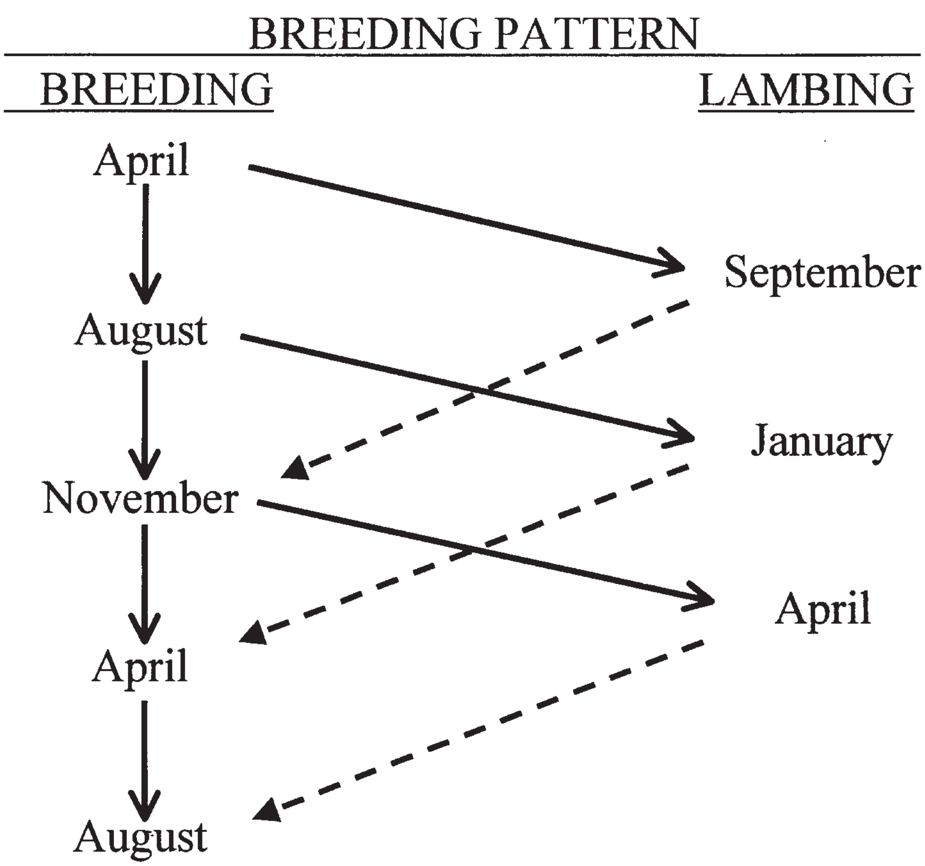

Figure 7. An example of a breeding schedule for three lambing opportunities in 2 years, from Notter and Copenhaver (1980). Solid lines designate the possible movement of open or pregnant ewes after breeding. Dashed lines indicate the pattern of return to breeding after lambing. ©J. Anim. Sci. 51:1034.