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THE ASSOCIATION BETWEEN VARIATION IN THE SEASONAL ONSET OF OESTRUS AND LITTER SIZE IN THE EWE

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Summary. The relationship between the date of first oestrus of the breeding season and litter size when mating took place at the first, second, third, fourth or fifth oestrus was studied in 160 Polled Dorset Horn ewes which conceived to their planned mating. The ewes were maintained in one flock with vasectomized 'teaser' rams at a ratio of less than thirty ewes to one ram. Checks were made twice daily for ewes in oestrus. At first oestrus, ewes were allocated to be mated at their first, second, third, fourth or fifth oestrus. Ewes to be mated were withdrawn from the flock and penned with a ram for 2 days. All live-births, stillbirths and premature stillbirths were recorded.

The previously reported pattern of low litter size from matings at the first oestrus rising to a peak at the third oestrus was found. There was an indication that ewes exhibiting first oestrus late relative to other ewes in the flock had lower litter sizes, irrespective of the oestrus at which they were mated. Ewes which exhibited first oestrus early showed no seasonal rise in litter size. Ewes with a later onset of oestrus showed an increase in litter size with successive oestrous periods.

INTRODUCTION

Within breeds of sheep, the range of the date of onset of seasonal oestrus between individual ewes is often as large as 75 days in a single environment (Hafez, 1952a, b; Hutchinson, O'Connor & Robertson, 1964; Lees, 1966). This range is partly a consequence of variation in the previous history of the ewe, for example date of lambing (Lees, 1966), partly individual physiological variation in response to environmental stimuli, which are mainly photoperiodic, and partly individual variation of endogenous rhythms of physiological activity affecting the onset of the breeding season. It seems reasonable to propose that factors leading to variation in the date of onset of oestrus may also determine variation in other reproductive characters such as the length of the breeding season, the number of ova shed at each ovulation and litter size, but few investigations have been reported which indicate relationships of this kind. Williams, Garrigus, Norton & Nalbandov (1956) reported that ewes showing their first seasonal oestrus early had a greater chance of having an abnormal length of cycle than did ewes showing their first oestrus late. Abnormal cycles were defined as outside the range of 14 to 19 days. Kelley & Shaw (1943) and McKenzie & Terrill (1937) showed that the earlier the onset of the breeding season, the longer the season. Hafez (1952a, b) suggested positive relationships between the duration of the oestrous cycle and the duration of oestrus and between the latter and the number of oestrous cycles in the breeding season. Land (1970) found a positive relationship between the duration of oestrus and litter size, both between and within breeds.

For flocks of ewes, the seasonal change in litter size depending on time of mating has been established as a gradual rise from early to mid-season followed by a gradual decline to the end of the breeding season. The early literature on this subject has been reviewed by Reeve & Robertson (1953). Later, Averill (1955) and McDonald (1958) showed a similar change for ovulation rate, but, McDonald's data also indicated an early season peak ovulation rate in the 2nd week of the breeding season. These observations were presumably on ewes showing first oestrus early, and, since very few were involved, their significance was not established. Similar observations on high litter size in ewes mated very early (Hammond, 1944; Averill, 1959; Quinlivan & Martin, 1971) have been largely ignored by other workers because few ewes were involved in each case.

In all experiments so far reported in which the relationship between litter size and season of mating has been investigated, the time of onset of the breeding season of the ewe and the number of oestrous periods before mating the ewes have been confounded. The purpose of the study reported here was to estimate the relationship, if any, between each of these factors and litter size.

MATERIALS AND METHODS

A total of 192 Polled Dorset Horn ewes aged between 1½ and 4½ years at mating were available for the study. The ewes of 2½ years and older that had lambed during the previous lambing season, had done so between 2nd February and 8th April, 1969, except for one ewe which lambed early on 1st January 1969. The lambs of all ewes were weaned on 21st May 1969. None of the 1½-year-old ewes had lambed during the 1969 lambing season.

Vasectomized teaser rams were kept with the ewes (as one flock) from 5th July 1969, at a ratio of at least one ram to thirty ewes, and observations were made twice a day to detect the first signs of oestrus. The first oestrus was detected on 24th July and other ewes, with one exception (16th October), showed first oestrus on following days up to 19th September, a range of 58 days. At the time first oestrus was detected, ewes were allocated at random to be mated at their first, second, third, fourth or fifth oestrus, so that matings within each oestrus showed a similar frequency distribution in time to the distribution of first oestrus. As soon as the appropriate oestrus was detected, the ewe was placed in a pen with a Finnish Landrace ram for up to 2 days. Only one ram was used over the mating period to avoid any ram fertility differences. Because of the protracted mating period, the ram was never required to mate with more than seven ewes per day, and usually with four or fewer per day. Subsequently, the ewes were run with a Dorset Down ram so that ewes which did not hold to first service and which were mated again at a later oestrus could be easily identified at lambing by the face colour of the lambs.

The ewes were not weighed until lambing; there was, therefore, no information on liveweight changes during the mating period of 4 months. The ewes rotationally grazed approximately 30 acres of long ley ($6\frac{2}{3}$ ewes per acre) until early October when those ewes already mated were moved. The late mated ewes did not appear to lose body condition and it is assumed that the influence of liveweight change on the ewe's performance was negligible.

At lambing, all normal live births, stillbirths and premature stillbirths were recorded.

RESULTS

The following analyses consider only the 160 ewes which conceived to their planned mating, because those ewes which did not conceive may have done so

Table 1. Dates of previous lambing, dates of onset of oestrus and litter sizes within age groups for all mating cycles for ewes lambing to a designated oestrus*

Age of ewe at mating	*Date of previous lambing*		*Date of onset of oestrus*		*Litter size*	
	Mean ± S.E.	*No. of ewes*	*Mean ± S.E.*	*No. of ewes*	*Mean ± S.E.*	*No. of ewes*
$4\frac{1}{2}$ years	67·7 ± 9·9	6	232·5 ± 2·2	8	1·25 ± 0·16	8
$3\frac{1}{2}$ years	59·0 ± 18·2	4	226·4 ± 2·5	5	2·00 ± 0·32	5
$2\frac{1}{2}$ years	70·0 ± 1·6	39	230·0 ± 1·8	55	1·55 ± 0·07	55
$1\frac{1}{2}$ years			231·2 ± 1·1	92	1·51 ± 0·06	92
Ewes not conceiving to planned mating	71·6 ± 3·8	21	231·8 ± 1·9	32		

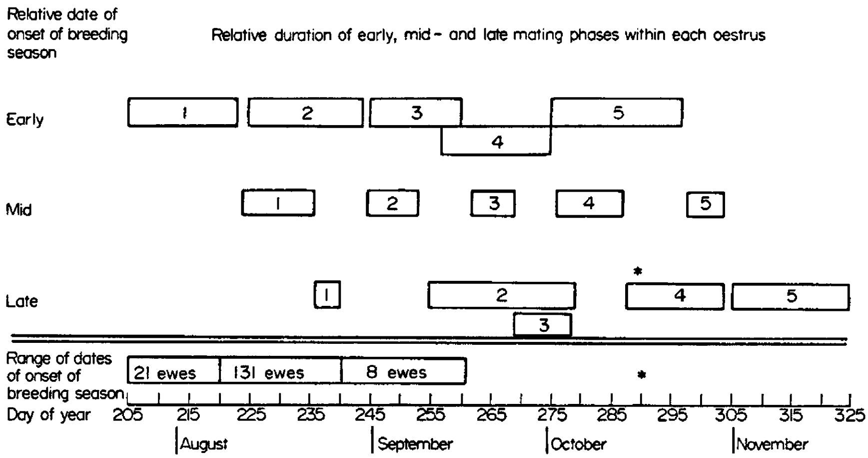
* Dates calculated from Day 1, i.e. 1st January 1969.

by chance or may have been less fertile than others. The conception rates at each oestrus, judged by returns to service and lambing dates, were 89%, 80%, 94%, 64%, and 84% at the first to the fifth oestrus, respectively. There appeared to be no consistent change in fertility due to the number of oestrous periods or to the use of one ram. Amongst ewes which failed to conceive to their planned mating, there was no relationship with date of mating; unsuccessful matings were distributed throughout each oestrous period.

Before examining the data for a relationship between date of oestrus and litter size, it had to be established whether the observed date of first oestrus was influenced by previous reproduction and management. In this study, date of previous lambing and age of ewe were factors that could have influenced the date of first oestrus. For all analyses, the dates of lambing, dates of first oestrus and dates of mating were related to Day 1, i.e. 1st January 1969.

There was no difference in date of onset of oestrus between the $2\frac{1}{2}$-year-old and older ewes which lambed during 1969 and those that did not lamb, the means ± S.E. were 229·7 ± 1·9 and 230·0 ± 1·7 from forty-nine and nineteen ewes, respectively. Amongst the ewes that had lambed, the range of lambing dates was too small to show any relationship between date of lambing and subsequent date of first oestrus. The regression of date of first oestrus on date of lambing gave a coefficient of 0·04 ± 1·12 (r = 0·05). Previous reproduction did not, therefore, influence the onset of the breeding season. The date of previous lambing, date of onset of oestrus and litter size for ewes of different ages are shown in Table 1.

The distribution of age groups within all five oestrous periods was similar. The overall age-group means in Table 1 were assumed to be reliable indications that no age effects confounded subsequent analyses, and therefore the data from all age groups were pooled.



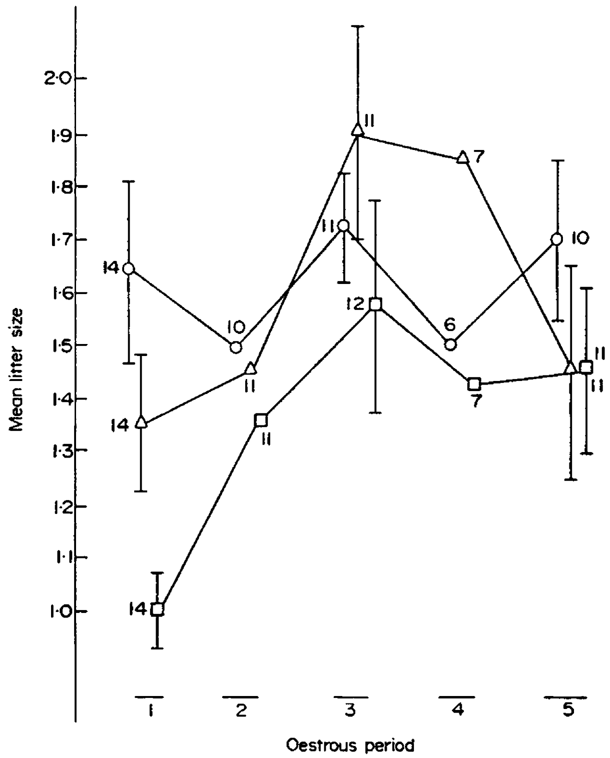
TEXT-FIG. 1. The time relationships between the dates of the first oestrus of the breeding season and early, mid- and late phases of mating of ewes within each oestrus. The diagram is based on data from those ewes which conceived as a consequence of mating at the selected oestrus. *One ewe showed first oestrus exceptionally late but mated at this oestrus.

To examine the effect of date of onset of the breeding season on litter size, the data for each oestrus were divided into three phases, early, mid, or late, according to the dates on which the ewes exhibited first oestrus. This is illustrated in Text-fig. 1. The determination of the phases was accomplished by two arbitrary methods. The first method was to divide the time period over which mating took place within each oestrous period into three equal time periods (Text-fig. 1, lower part). Due to the nature of the distribution of ewes in each oestrous period, however, this resulted in too few ewes in early and late phases. The second method was to separate the ewes mating at each oestrus into three groups so that the early, mid- and late phases within each oestrous period were represented by a similar number of ewes (Text-fig. 1, upper part).

To check that the durations of the phases selected did not influence the results of subsequent analyses, four sets of early, mid- and late phases were chosen and compared.

The mean litter size within each phase of each oestrus was calculated for all the above methods of phase determination. All analyses indicated a similar relationship between litter size and the phase of mating. The analysis with similar numbers of ewes per phase is presented as representative.

Text-figure 2 shows the mean litter sizes and the distribution of ewes for the early, mid- and late phases of each oestrus. Significant increases in litter size occurred over the first three oestrous periods for ewes mated during the mid- and late phases ($P < 0{\cdot}05$, as tested by Student's t test). Ewes showing consistently early oestrus, had consistently high litter sizes from matings at their first to fifth oestrous periods.



TEXT-FIG. 2. Mean litter sizes in early (○), mid- (△) and late (□) mating phases in the first to fifth oestrous preiods of the breeding season. The vertical bars indicate standard errors of means. The figures represent the number of ewes contributing to the mean.

Oestrus and phase differences in litter size and the apparent interaction between them were studied further by analysis of variance. The analysis was conducted between oestrous periods and between phases within oestrous periods. The interaction between oestrus and phase was also included in the model. The analysis is shown in Table 2. The interaction was not significant so the main effects were tested for significance, omitting the interaction from the model. The analysis allowed for unequal sub-class numbers, and oestrous period and phase means were calculated and corrected for disproportionate representation. The corrected means for each oestrus are shown in Table 3 and for each phase in Table 4.

The analysis of variance showed significant differences between phases and between oestrous periods. Mean litter sizes from matings in late phases were significantly lower than from matings in early phases (Table 4) and the mean litter size from matings at the third oestrus was significantly greater than that from matings at the first oestrus (Table 3).

Table 2. Analysis of variance for the effects of oestrus and phase of mating on the litter size of ewes

Source of variation	*d.f.*	*Mean square*	*F*
Between oestrous periods	4	0·7780	2·78*
Between phases within oestrous periods	2	1·0818	3·87*
Interaction, oestrus + phase	8	0·2472	0·87
Residual	145	0·2011	
Pooled residual	153	0·2794	

* F ratio significant at $P < 0{\cdot}05$.

Table 3. Litter sizes from matings of ewes within each oestrus corrected for disproportionate representation of phases

	Oestrous period					*Pooled S.E. of differences between means*
	1	2	3	4	5	
Mean litter size	1·36	1·44	1·74	1·62	1·53	0·14
No. of litters	42	32	34	20	32	

Table 4. Litter sizes from matings of ewes within each phase corrected for disproportionate representation of oestrous periods

	Relative date of mating (phase)			*Pooled S.E. of differences between means*
	Early	*Mid*	*Late*	
Mean litter size	1·64	1·60	1·37	0·10
No. of litters	51	54	55	

DISCUSSION

The results of this study are in accord with earlier studies to the extent that, on a flock basis, litter size increased progressively from matings at the first to third oestrus within a breeding season and declined at the fourth and fifth oestrus. The observations of particular interest in this study, however, concern litter size in relation to date of onset of the breeding season. Study of the separate effects of date of onset of the breeding season and of number of oestrous periods before mating on litter size suggested that ewes with a relatively early onset of the breeding season had litter sizes which were above or equal to the average for the whole flock, irrespective of the oestrus at which they were mated. There was no evidence that their litter sizes increased or decreased from matings over the first five oestrous cycles of the breeding season. Ewes with a relatively late onset of the breeding season had litter sizes which were consistently, sometimes significantly, below the flock average. These ewes, and to a lesser extent those with average times of onset of the breeding season, showed increases in litter sizes from matings at the first to third oestrus and smaller litter sizes at the fourth and fifth oestrus.

Litter size is determined not only by ovulation rate but by fertilization, implantation and embryo mortality rates. It is possible that all these factors may be associated with variation in the dates of first oestrus in a similar manner to litter size. That litter size reflects ovulation rate to a large degree is evident from recent American and Australian research involving laparotomy (e.g. Hulet & Foot, 1967; Fletcher & Geytenbeek, 1970).

If litter size reflects the ovulation rate, it seems that ewes showing oestrus early reach peak ovulation rates at first oestrus or at 'silent' ovulations before the breeding season while ewes which come into oestrus later reach peak ovulation rates during the breeding season. If the observed variation in onset of oestrus also exists in onset of ovulation, ewes showing first oestrus late would appear to need a higher number of ovulatory cycles before reaching peak ovulation rates. Ewes showing late oestrus, however, may not have as many pre-breeding season 'silent' ovulations as ewes showing early oestrus. Further information is needed on this aspect.

The results of the present study suggest three possibilities concerning the relationship between date of first oestrus and litter size. Inherent differences between ewes in reproductive capacity, implying a genetic correlation between the date of first oestrus and litter size, may exist. Dutt & Woolfolk (1968) reported some progress in selection for earlier lambing. They attributed the earlier lambing to an earlier display of first oestrus and were able to demonstrate a concurrent rise in lambing percentage. Ewes were not selected on the basis of litter size although some culling of barren ewes occurred. By contrast, Purser (1972) found no genetic correlation between the onset of the breeding season and litter size.

An alternative cause may be the influence of an environmental factor affecting both onset of oestrus and litter size. Such a factor could be body weight or condition. The relationship between body condition and litter size is established. The authors have unpublished information that ewes in good body condition show an early date of first oestrus.

The relationship between an early date of onset of the breeding season and a high litter size may therefore be of environmental origin. The significant rise in litter size from first to third oestrus in ewes showing late oestrus may not be similarly explained as the nutritional conditions of these ewes remained constant over the mating period.

A third possibility is that non-genetic variation in ovulation rate may affect the production of oestrogen and progesterone. If the number of developing follicles or corpora lutea in the ovary influence the levels of secretion of oestrogen and progesterone, ovulation rate may affect the attainment of the required endocrine conditions for the display of oestrus.

Further work should be conducted under strict control of nutritional conditions to verify these results and to isolate the possible causes of the relationship described.

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