THE INFLUENCE OF SEASON AND NUTRITION
ON
OESTRUS AND OVULATION
IN
SOUTH AUSTRALIAN STRONG-WOOL MERINO EWES

by

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TABLE OF CONTENTS

SUMMARY

This thesis reports a study of the effect of season, and hence level of nutrition and body composition, on the incidence of oestrus and multiple ovulation among Koonoona strain South Australian strong-wool Merino ewes in a Mediterranean type environment. Experimental aspects of the study were conducted at Turretfield Research Centre, Rosedale, South Australia.

Previous experiments had been conducted to investigate relationships between nutrition and both oestrus and ovulation among groups of ewes restrained in small yards and offered various amounts of a hay/grain ration. Seasonal fluctuations in liveweight were eliminated.

Several pertinent questions arise if the results of these experiments are to be applied to the commercial situation where it is clear that sheep do experience annual fluctuations in nutrition, liveweight and body condition. In particular, would ewes experiencing 'normal' fluctuations in liveweight applied in the pen situation perform similarly to ewes maintained at steady liveweight? And would these ewes experiencing fluctuating liveweight in pens perform the same as their counterparts grazing in the field?

The study consisted of four main areas of investigation: to repeat the previous study, conducted at steady liveweight in pens, in a second year; to investigate the two questions mentioned in the previous paragraph; and to consider within-flock relationships between ovulation and water turnover, liveweight, body size and body condition.

The first area of investigation comprised a comparison, in autumn and spring, of the incidence of oestrus and ovulation of two groups of ewes offered a hay/grain ration and maintained throughout a year at a constant mean liveweight of about either 45 or 54 kg. In each group there was a clear annual fluctuation in the incidence of both oestrus and ovulation with a greater incidence occurring during autumn than during spring.

These findings not only confirm previous observations, made of similar ewes maintained at 49 kg, but extend them to cover the mean liveweight range between 45 and 54 kg. While this difference in liveweight did not affect the incidence of oestrus there was a greater incidence of multiple ovulation at the higher liveweight level.

The second area of investigation comprised a comparison of the performance of the two groups of ewes considered above with a third group of ewes offered a hay/grain ration, of the same composition, but of varying amount, such that they experienced an annual cycle of liveweight change. The change was similar to that commonly occurring among ewes grazing in the field in a Mediterranean environment. The oestrus and ovulatory activity of the fluctuating liveweight group, during both autumn and spring, was not significantly different to that of the appropriate sustained liveweight group of similar mean liveweight.

The third investigation comprised a comparison of the performance of the third hay/grain fed group of ewes with fluctuating liveweight with a fourth group of ewes grazed on pasture under commercial conditions and which experienced a similar fluctuation in liveweight. Both the oestrus and ovulatory performance of the groups was different. There was a lower incidence of oestrus during spring, and a greater incidence of multiple ovulation during autumn, among the ewes grazing pasture. The difference in the incidence of oestrus was less than may be expected for between-year variation and might not have represented a significant biological difference. The greater incidence of mutiple ovulation cannot be explained in a similar manner; nor can it be clearly explained on the basis of difference between the group means for body condition index or the body components fat, water, lean or protein.

However, in retrospect, there are three situations that indicate that the quality of the feed consumed may offer an explanation for the difference observed in multiple ovulation. Firstly, when compared over all treatments and seasons, there was a low but statistically significant correlation in the present study between the incidence of multiple ovulation and the estimated mean weight of body protein at ovulation. Secondly, a review of the literature concerning 'flushing' provided evidence that the so-called dynamic effect of flushing could be due to differences in feed quality and, thirdly, there have recently been reports that ovulatory performance of a group of ewes of given liveweight can be different depending on the quality of the feed consumed prior, and leading up, to ovulation. In some instances this difference has occurred without a concurrent significant change in mean liveweight. Such a situation could have occurred in the present study, as during autumn the field ewes were grazing fresh green pasture. This was very likely of higher quality than the hay/grain feed on offer to the confined group.

If the difference in multiple ovulation observed during autumn was indeed attributable to feed quality as suggested above then clearly this is an additional factor that must be accounted for in predicting the ovulatory performance of grazing ewes.

The final area of the study revealed a significant, positive, within-flock linear correlation of ovulation rate with both liveweight and body condition index, but not with body size. However, the partial correlation with either factor was insigifncant when variation due to the remaining factor was removed. Ovulation rate was almost equally well correlated with either factor in autumn, but was better correlated with body condition than liveweight during early spring. The study did not provide significant evidence of a correlation between ovulation rate and the rate of water turnover.

DECLARATION

This thesis does not contain any material previously presented or accepted for the award of any degree or diploma in a University. Nor, to the best of my knowledge, does it contain material previously published or written by any other person except where duly acknowledged.

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INTRODUCTION

I. INTRODUCTION

The reproductive performance of a flock of ewes (often regarded commercially as the number of lambs weaned per ewe present at joining) is the culmination of a series of circumstances and events in the reproductive process. These include the occurrence of behavioural oestrus, libido, mating behaviour, semen quality, ovulation, fertilisation, implantation, embryo mortality, abortion, and both parturient, and early post-natal, lamb death. With the exception of cleavage of the fertilised ovum to produce two zygotes (a rare occurrence) all these events act to reduce the performance of the flock below its potential, viz. the number of ova shed at joining.

The present study was confined to a consideration of factors affecting only two of the events in the reproductive process, namely, ovulation (the potential performance) and the occurrence of behavioural oestrus (the first event in the reproductive process that may reduce performance). The major factors considered that affect these two events were the season of joining and the level of nutrition (as reflected by the level and change in liveweight or body condition).

Ewes of many different breeds have been shown to exhibit seasonality in the period of the year over which they exhibit behavioural oestrus. The duration of this period - the breeding season - varies between breeds from two to three months (Icelandic sheep) to almost continuous (Dorset Horn, Merino, Prealpes). Changes in daylength clearly provide the over-riding modulus for the seasonality of those breeds with a restricted breeding season. Daylength becomes a less important modulator among breeds with a longer breeding season. In these breeds the introduction of rams and environmental temperature are two factors that assume greater importance.

The breeding season of ewes descended from South Australian strong-wool Merino rams has been studied in Queensland, New South Wales and Tasmania (Kelley and Shaw, 1943; Kelley, 1946). In this study extending over eight years, in which the ewes were continuously associated with rams (a situation where there is no stimulatory or synchronising effect of the presence of rams on the occurence of oestrus) the ewes exhibited definite breeding and non-breeding seasons. In one year a small number of ewes exhibited oestrus throughout the year, including the usual non-breeding season from October to December. Oestrous behaviour following the sudden introduction of rams was not examined. This situation, the common practice in commercial sheep husbandry, was considered in the present study.

It has been established, among British breed and British breed x Merino crossbred ewes, that an improved level of nutrition before, and during, joining will increase the incidence of multiple ovulation and multiple births. Coop (1966a) has defined two independent effects of nutrition on the incidence of multiple ovulation. The incidence is positively related to the level of liveweight at mating (static effect) and is increased by a state of increasing liveweight immediately prior to mating (dynamic effect). The degree to which nutrition modulates the incidence of multiple ovulation may depend on the season of joining (Fletcher, Geytenbeek and Allden, 1970).

The effects of nutrition on the incidence of multiple ovulation are not as clearly established among Merino ewes. Medium-wool strains have been studied on several occasions with variable findings. McInnes and Smith (1966) found that the incidence of twin births was increased by 'flushing' (i.e. there was a dynamic effect) but was unaffected by liveweight at mating (i.e. no static effect). Edey (1968) reported that the incidence of multiple ovulation was affected by liveweight at mating, but part of the variation in weight could have been attributed to differences in body size rather than solely to nutrition. Suiter and Fels (1971) also noted an association between pre-mating liveweight and the incidence of twin births. They obtained a significant interaction between pre-mating liveweight and the season of lambing (mating).

Detailed studies have only recently been undertaken to assess the effects of season and nutrition on the oestrous and ovulatory performance of 'Koonoona' strain South Australian strong-wool Merino ewes, under South Australian environmental conditions. Since 1969 a series of experiments, involving ewes from a 'Koonoona' based flock, have been conducted at Turretfield Research Centre, Rosedale, South Australia.

In the first experiment, conducted during 1969, Fletcher (1971) studied the relation between the incidence of multiple ovulation and the level of nutrition provided during the previous six weeks. He concluded that the incidence was directly related to the mean liveweight at ovulation and increased by 2.5% for each kilogram increase in mean liveweight over the range from 42kg to 55kg. However, the incidence of multiple ovulation was unaffected whether liveweight increased, decreased, or remained steady during the six-week treatment period. Similar sets of observations were made during summer (January) and autumn (April) but there was no effect of season on the liveweight - multiple ovulation relationship.

A second experiment was conducted to investigate the effect of season on the incidence of behavioural oestrus, the level of ovulation (ovulation rate) and lambing performance. One of eight randomised groups of ewes were joined with entire rams at each of eight times spread evenly throughout the period from April 1970 to February 1971. Each group was joined at a similar liveweight - the normal seasonal fluctuation in liveweight having been suppressed by confining the ewes in a small yard and offering them regulated amounts of a hay/grain ration. This experiment clearly showed that there was an annual cyclic variation in the incidence of multiple ovulation, with the incidence being greatest during summer and early autumn, and lowest during winter. There was a marked seasonal variation in the incidence of behavioural oestrus detected in the first 14 days of joining (approximately one oestrous cycle length) with almost 100% of the ewes being detected during summer and as low as 25% during late winter and early spring. While the percentage of lambs born (per ewe present at lambing) followed a similar, but obviously out of phase, seasonal pattern to that of ovulation rate there was not a clear effect of season on the percentage of lambs weaned. This was due partly to a lower survival rate among the lambs born during winter and early spring and also to the large error of each estimate resulting from the small number of lambs weaned in a group (13 to 26). There was little seasonal variation, however, in the incidence of oestrus detected to day 35 of joining when almost all ewes in each group had exhibited oestrus. Those groups with a low incidence to day 14 showed a marked synchronisation of oestrus during the third and fourth weeks of joining.

South Australia experiences a Mediterranean type climate with, typically, a large proportion of the annual rainfall occurring during the period from May to October. Thus there is a plentiful supply of green feed available to the animals for five or six months of the year and then diminishing amounts of dry residue for the remainder of the year. In these circumstances grazing animals undergo an annual cycle of liveweight change. At Turretfield liveweight normally rises from late June until the end of November, remains constant during December and then falls steadily from January until May. While it is customary to provide supplementary feed (cereal grain and/or hay) during the autumn this practice, although reducing the magnitude of the annual fluctuation in liveweight, does not usually arrest the decline completely.

From the two experiments mentioned above it appeared that, following the sudden introduction of rams, Koonoona ewes exhibited behavioural oestrus at any season of the year and that, during summer and autumn at least, the incidence of multiple ovulation increased with increasing liveweight at ovulation. However, both the oestrous and ovulatory performances were based on observations made in one year only. Also, in both experiments the ewes were confined in small yards and fed a hay/grain ration. In view of the between-year, and within-year, variation in climate and nutritional conditions the usefulness of these findings to the commercial situation was questionable on two grounds. Would the performance be repeatable in other years? Would the performance observed in the pen situation be applicable in a grazing situation?

Two aims of the present study were directly related to the above questions. They were firstly, to confirm and extend to two liveweight levels the previous findings of oestrous and ovulatory performance observed under pen conditions, and secondly, to assess and compare the performances under field conditions with those observed in the pen situation.

Confirmation of the previous findings were attempted at only two times of the year, namely, at the expected time of highest (March/April) and lowest (September) ovulatory performance. The experimental techniques used differed from those employed previously, too. This time each group of ewes was observed repeatedly. Oestrus was detected using vasectomised rams while ovulation was determined using the, then, recently available technique of endoscopy (Roberts, 1968) rather than laparotomy (Cutten, 1970). It was assumed that the presence of vasectomised rams for five or six weeks and/or endoscopy at one time of observation would not influence observations made five to seven months later.

As additional variables may affect the performance of grazing ewes compared with penned ewes a third aim of the study was to consider whether other factors, in addition to liveweight, could be measured and used to improve the prediction of ovulatory performance in the field, or even possibly the pen, situation. Body condition was one obvious factor, as the condition of grazing ewes varies widely throughout the year and is known to be correlated with ovulatory performance (Gunn, Doney and Russel, 1969; Bastiman, 1972; Gunn and Doney, 1975). Accordingly body condition at ovulation was assessed using liveweight as a proportion of body size as an index (Guerra, Thwaites and Edey, 1972a). The possibility of gross differences in body composition was also considered and the components of fat, lean, protein and water were measured in a sample of ewes from each group using prediction equations based on tritiated water studies (Searle, 1970b).

The final aim of the study was to consider the within-flock relationship of each of several factors with ovulation rate. Firstly, Fletcher (1971) reported a within-flock relationship between the incidence of multiple ovulation and what he termed 'inherent liveweight'. The present study extends those investigations to consider the relationship not only with liveweight but also with its components, body size and body condition.

Secondly, Macfarlane, Dolling and Howard (1966) reported that high wool producing ewes had high water turnover. They suggested that the increased wool production may correlate with the cellular use of water in intermediary metabolism and relate to total energy turnover. Graham (1968) observed that rams from the high producing group had a higher metabolic rate than rams from the low wool producing group. If these suggestions are correct then the possibility exists that other bodily functions, including the level of hormone production, could also be higher, and specifically there could be a correlation between water turnover and ovulation rate. Therefore a number of measurements of turnover were made and the data were examined for a relationship between turnover and ovulation.

LITERATURE REVIEW

OESTRUS

II. LITERATURE REVIEW

A. THE EFFECT OF SEASON, THE PRESENCE OF RAMS, NUTRITIONAL STATUS AND BODY SIZE ON THE OCCURRENCE OF OESTRUS IN EWES

1. INTRODUCTION

The breeding season of wild sheep in the Northern Hemisphere is generally restricted to the autumn months of October, November and December (Hafez, 1952) and it seems that its duration is related to the geographic origin of the species or breed. Those types originating at higher latitudes have a more restricted breeding season than those originating in a more equatorial region (Yeates, 1949; Hafez, 1952).

During the process of domestication there have been changes in the distribution, type of production and management of sheep populations. From experiments conducted in widely differing localities and with different breeds (Roux, 1936; McKenzie and Terrill, 1937; Thompson, 1942; Kelley and Shaw, 1943; Hammond Jr., 1944; Phillips, Schott and Simmons, 1947) it is apparent that many breeds have a breeding season extending over the autumn and winter months and are anoestrus in spring and early summer. This restriction in breeding season is not considered to be a disadvantage in some regions, such as in Great Britain, but in other areas - some parts of Australia (Nichols, Shier and Roberts, 1938), South Africa (Roux and Van Rensburg, 1935) and in U.S.A. (Henning and MacKenzie, 1927) - pasture and climatic conditions are more favourable for the survival and growth of young lambs born in autumn or early winter.

Therefore it is necessary that the ewes breed in late spring or early summer. This has resulted in the use of breeds with long breeding seasons and also in active selection for early breeding.

Thus there is now a range of types of domestic sheep from those with very short breeding seasons of only one or two months as in some indigenous sheep of the arctic or near arctic region (Yeates, 1949; Hafez, 1952) to others - notably Ogaden, Karakul, Dorset Horn and some strains of Merino (Hafez, 1952), Corriedale, Ile de France and Prealpine (Ortavant, Mauleon and Thibault, 1964) - that will breed during most or all of the year.

2. OESTRUS AND SEASON

(a) Introduction

It has been known for a long time that there is a well defined seasonal rhythm in the breeding of many birds and mammals and this was generally thought to be controlled by seasonal fluctuations in temperature. However, Rowan (1925) was able to obtain marked gonadal development in juncos several months earlier than normal by the use of additional artificial light during the early winter with no alteration to the temperature experienced by the birds. Investigations into the effect of the light environment on sexual rhythm were later extended to mammals. Bissonnette (1932) induced full oestrus in ferrets some months before the expected time, by using 6 hours of artificial light in addition to the normal winter daylight hours, while Baker and Ransom (1932) concluded that light was an important factor in the control of sexual activity of the field mouse. The early literature has been reviewed by Rowan (1938) and by Marshall (1942). At that time it was fairly clear that in the majority of seasonal breeding animals investigated, the rhythm of breeding was controlled, to a large extent, by the seasonal changes in the length of daylight and darkness.

In general the breeding season of ewes is evenly spaced on either side of the shortest day of the year (Hammond Jr., 1944; Yeates, 1949) and it is well known that this is primarily controlled by the annual cycle of natural daylength (Yeates, 1949). However, seasonal changes in other environmental factors, notably temperature, are known to modify the precise timing of the onset and cessation of the breeding season (Dutt and Bush, 1955).

(b) Daylength

Marshall (1937) noted that sheep transported across the equator from one hemisphere to another reversed the time of year at which they bred, so that they conformed with the new seasons. He suggested that decreasing daylength could be the stimulus for this although he pointed out that temperature might also be involved. Definite evidence of the importance of daylength was not available until the report of Yeates (1949). In his experiments conducted at Cambridge (52°N), Yeates subjected Suffolk x Border Leicester-Cheviot ewes to exaggerated reversed seasonal changes in daylength varying from 21 to 5.5 h daily. The ewes were allowed to graze during the day and only confined to their pens as required to adjust the length of daylight. Control animals were also penned at the same times in the open. Yeates showed that the onset of the breeding season was a direct consequence of the change from increasing to decreasing length of daylight and that it occurred approximately 13-16 weeks after the change to decreasing daylight. This took place whether the change in light trend began at the level of 21.5, 18.5, 15 or 13.5 h of light per day, with oestrous activity beginning at levels of 13.5, 9.5 and 6 h light per day. Yeates also found that the end of the breeding season occurred within 14 to 19 weeks after a change from decreasing to increasing daylength. Again this was independent of the length of daylight at which the change in trend occurred and at which oestrus activity ceased. Within the limits of the observations temperature did not exert any influence on the breeding season.

Since this initial work by Yeates the importance of daylength in controlling the breeding season has been demonstrated in the Dorset Horn breed and in a number of Mountain breeds in the U.K. (Hafez, 1952), in Peppin Merinos in Queensland (Yeates, 1956) and in Southdown ewes at Armidale in New South Wales (Thwaites, 1965).

Daylength control is related to the ratio of light to dark and is not dependent on there being a gradual change like that occurring naturally. Hart (1950) found that when Suffolk ewes (at Cambridge) were subjected to an abrupt decrease in daylight to a constant ratio of 1 light : 2 dark oestrous activity resulted regardless of whether the schedule each 24 h was 4 h light, 2 h dark, 4 h light, 14 h dark, or 4 h light, 8 h dark, 4 h light, 8 h dark. Hafez (1952) also found that abrupt changes in daylength were effective in stimulating oestrus in Dorset Horn, Welsh Mountain x Dorset Horn, Suffolk, Romney Marsh, Border Leicester, Blackface Mountain and Welsh Mountain ewes studied at Cambridge.

The period of time between the change of light regime and the beginning of the breeding season (latency of initiation) has been found to differ markedly in ewes of the same breed observed at different times (Hafez, 1952). Hart (1950) reported a latency of initiation of 30 days in Suffolk ewes given a treatment of 4 h light, 8 h dark, 4 h light, 8 h dark, while Hafez (1952) reported a period of 168 days for ewes from the same flock given the same treatment. The latency of initiation may be affected by the age of the animal – young animals appear to be influenced more easily (Hafez, 1952) ; by the time of the year at which the treatment starts – ewes in shallow anoestrus responded more quickly than those in deep anoestrus (Hart, 1950; Ducker and Bowman, 1970b); and by the nature of the light treatment – bigger increases in light cause more rapid response (Ducker, Thwaites and Bowman, 1970). There are also wide differences between individuals. The effect of artificially changing day length has recently been summarised concisely by Ducker and Bowman (1974).

In addition to the within-breed variation mentioned there are breed differences in latency of initiation. Hafez (1952) found that the Dorset Horn and its cross had a much shorter period of latency than any of the other Mountain breeds he compared.

The latency of cessation, that is the average period of time between the start of the inhibiting light treatment (long days) and the last oestrus of the breeding season, while often being less variable than the latency of initiation is nevertheless influenced by the same factors. The effects are reversed, however; breeds that have a short latency of initiation have a long latency of cessation. This inverse relationship between latency of initiation and latency of cessation is not always symmetrical, with the result that mid-breeding-season date can be some days before the shortest day of the year.

The nature of the daylength change imposed has clearly been shown to affect the latency of both the initiation and cessation of oestrous activity, in ewes with a breeding season of either short or moderate duration. Clun Forest ewes had a shorter latency of initiation following a large abrupt decrease in daylength, or a rapidly decreasing artificial daylength, than following a smaller or slower decrease (Ducker *et al.*, 1970). These ewes also had a shorter latency of cessation following a large or rapid increase in daylength than following a more gentle increase (Ducker and Bowman, 1970a).

The timing of the daylength change (in relation to the normal breeding season) also affects the duration of the latency. Ducker and Bowman (1970b) applied similar light treatments at different times and found that the latency of initiation was shorter in ewes stimulated (short days) near the end, rather than the beginning, of their normal season of anoestrus. Hafez (1952) found that the latency of cessation was shorter when long day treatment was applied at the beginning, rather than the middle, of the breeding season.

The influence of the nature of daylength change on ewes that have a long breeding season is not clear. Dorset Horn ewes exhibit oestrus soon after the longest day (Hafez, 1952) and some Merino ewes cycle before the longest day (Watson and Radford, 1955). Decreasing light is apparently unimportant in these ewes.

(c) Inherent rhythm

While there was comment and speculation by a number of authors about the possibility of a "fundamental rhythm of sexual activity" before and including Yeates (1949), it is only since then that experiments have been conducted that provide some definite evidence.

These studies have all been designed to suppress the modulating effect of variation in daylength and have involved the use of a set daily lighting pattern on a continuing basis for an extended period of time. This has usually involved the use of either continuous, equatorial, or short day (about 6 or 8 h light) light regimes.

(i) Continuous and long-day light

The first experiment conducted using a set light regime was that of Hafez (1952) who used a long-day of 16 h. He found that ewes of a number of British breeds ceased activity when first exposed to long days but that they became active again 4-6 months later. Dorset Horn ewes, however, remained active throughout the treatment period although they did show an increased incidence of silent ovulations (ovulation without oestrum).

A more detailed study has been made of medium-wool Merino ewes exposed to continuous light for two years (Radford, 1961a). These ewes, three months old at the beginning of the treatment, showed some suppression of oestrus during the first year when they were 8-9 months old, and greater variability in the length of the sexual season during the second year. There was no apparent suppression of ovulation at any time.

(ii) Equatorial light

Continued exposure to equatorial light has been investigated in several experiments. In an experiment conducted at Tooradin in Victoria (38^{o}S) Radford (1961b) subjected medium-wool Merino ewes, 2½-year-old at the beginning of the treatment, to two years of equatorial light. He observed variable response in sexual activity: some ewes continued to exhibit seasonal variation in activity while others exhibited continuous activity. Those ewes that experienced periods of anoestrum did so at the same time of the year as control ewes but the periods were of shorter duration.

A number of studies have been made in which short season breeders have been subjected to an equatorial light regime. Southdown ewes studied at Armidale, New South Wales, from the age of 1½ or 2½ years lost their seasonal breeding pattern after one year (Thwaites, 1965). Oestrous activity of individuals then became sporadic and on a group basis activity was much lower than in the control group although this low level did continue throughout the year. Wodzicka-Tomaszewska, Hutchinson and Bennett (1967) also found that Southdown ewes lost their seasonal rhythm after a period of equatorial light. However, in this instance rhythm was not completely lost until the ewes had experienced 2½ years of the treatment: a response not markedly different to the Merino ewes (long season breeders) observed by Radford (1961b). About two thirds of a flock of Border Leicester ewes (short season breeders) observed at 51^{O}N were found to remain anoestrus for a full year when subjected to equatorial lighting, beginning at the onset of their anoestrous period (Williams, 1974). Border Leicester ewes at Armidale (30^{O}C) have also shown a low incidence of oestrous activity under equatorial light. Their performance was somewhat improved by a period of continuous light during December and the first half of January (Williams and Thwaites, 1974).

Williams (1974) compared the performance of Border Leicester and Welsh Mountain ewes under both natural light (51^{O}N) and equatorial light (13 h light, 11 h dark). The two breeds performed similarly under natural light but significantly more Border Leicester ewes remained anoestrus throughout the year when exposed to equatorial light. Williams concluded that breeds normally exhibiting a short breeding season may show a marked difference in their response to equatorial light.

(iii) Short-day light

Continued short-day lighting (6 h light, 18 h dark) has been examined in an experiment conducted over three years in California, U.S.A., using Suffolk and Hampshire ewes ranging in age from two to six years (Clegg, Cole and Ganong, 1964). The experiment began at the end of the anoestrous period (August). The period of sexual activity was prolonged and the anoestrous period was shortened. Oestrous cycles became progressively less regular and rarely exceeded 50% of the cycles theoretically possible. Nevertheless, cyclic sexual activity continued for the duration of the experiment.

It is possible that seasonal changes in environmental factors other than daylength could modulate the seasonality of the breeding season when ewes are exposed to a set daily light regime over an extended period. Temperature is the most obvious factor, and has been investigated by Wodzicka-Tomaszewska *et al.* (1967) while light intensity has been suggested as another possible factor (Radford, 1961a). Wodzicka-Tomaszewska *et al.* (1967) applied reversed thermal seasons to both Southdown and Peppin Merino ewes subjected to continued equatorial light. They found that this treatment neither changed the timing of sexual activity to that produced by reversed photoperiod nor maintained regularity of the breeding season over an extended period.

They concluded that environmental temperature was not effective in modulating sexual activity. There do not appear to have been studies of reversed thermal seasons under other continuing light regimes.

Radford (1961a) found that ewes subjected to continuous light made up of natural light (varying in seasonal intensity) by day, and artificial light by night, showed greater seasonality of sexual activity than ewes subjected to continuous artificial light of constant seasonal intensity. He concluded that at least part of this difference was due to seasonal changes in light intensity. As there were only five ewes in each group this conclusion should be accepted with caution.

The evidence outlined above, covering continuing daily light regimes ranging from continuous light to 6 h light per day, indicates quite clearly that, in a number of breeds, most ewes that have already experienced seasonal sexual rhythm will continue to do so when they are denied seasonal variation in daylength. The most obvious other environmental factor, temperature, appears to play no part in modulating seasonal sexual activity. Thus the seasonality observed in the absence of daylength changes could be modulated by previous experience, by an inherent rhythm, or by environmental factors so far unexamined. Previous experienced of seasonal sexual activity has been found to be unnecessary in the case of continuous light (Radford, 1961a) and must therefore be of doubtful importance. Thus, unless environmental factors, such as atmospheric pressure or variation in the earth's magnetic field, have an influence, it seems that there may well be an "inherent rhythm", the modulating power of which is very much less than that of changes in daylength.

(d) Temperature

While seasonal changes in environmental temperature do not appear to modulate the regular occurrence of oestrus and anoestrus there is evidence that low environmental temperature can modify the timing of the onset of the breeding season (Dutt and Bush, 1955). Two groups of two- and three-year-old, parous Hampshire x Western ewes were maintained by hand feeding a hay and grain mixture in large sheds open to natural light in Kentucky, U.S.A. One group was exposed to natural temperature while the other was maintained at a constant temperature (7.2 - 8.9°C) and humidity (70%) in an air-conditioned room. Ewes subjected to the cold treatment from May 26 exhibited first oestrus, on average, 46 days later (July 10) while the mean date of first oestrus for the control ewes was September 2. While this is a substantial effect it should be noted that the treatment applied was very severe in comparison with the natural conditions prevailing at the time when the average daily maximum temperature for June, July and August was 31.5°C. Neville and Neathery (1970) reported that a difference of 5°C in summer temperature altered the onset of oestrus by 8, 4 and 16 days in three consecutive years. However, it should be noted that the temperature difference was obtained by grazing the ewes at different sites that differed not only in temperature but also in altitude. The effect could have been due to atmospheric pressure (see following section) or a combination of temperature and pressure.

Yeates (1953) examined the effect of high temperature on the onset of the breeding season in Romney Marsh ewes at Brisbane, Queensland. He found that confining ewes to a hot room maintained at 40.5°C dry bulb and 30.5°C wet bulb for 6 hours each week day from about 6 weeks before the onset of the breeding season did not influence its onset.

There do not appear to be any experiments investigating the effect of either high or low environmental temperature on the cessation of the breeding season.

(e) Atmospheric pressure

There is no direct evidence available, but several pieces of circumstantial evidence suggest that changes in atmospheric pressure may influence the timing of the breeding season. Ewes from two different origins have been observed over two years at each of two sites - one in Texas and the other in Idaho. Ewes of both origins became, and ceased to be, anoestrus up to two months earlier in Texas than in Idaho (Hulet, Shelton, Gallagher and Price, 1974). As this change was not symmetrical with changes in daylength and temperature they concluded that neither of these factors could be responsible. They pointed out that the Texas site was at an elevation of 213 m compared with 1 707 m at the Idaho site and suggested a possible effect of atmospheric pressure with high pressure advancing the season (there was also about 15^{o}C difference in temperature). A similar relationship has been suggested to explain the apparent later onset of the breeding season of Romney ewes at high altitudes in New Zealand (Quinlivan and Martin, 1971, 1972). Hafez (1952) states that "it is well known among Welsh farmers" that Welsh lowland sheep come on heat earlier than mountain sheep. He reports a similar situation between the lowlands and highlands of Scotland.

3. OESTRUS AND THE PRESENCE OF RAMS

(a) Length of the breeding season

In determining the effect of the presence of rams on the oestrous activity of ewes it is necessary to consider their behaviour in each of three situations. Namely, when running in continuous association with rams, when being suddenly associated with rams at a particular season of the year after being separate for the greater part of the year and when running completely separated from rams over an extended period.

(i) Continuously associated with rams

The approximate duration of the breeding season of Merino ewes run continuously with rams has variously been reported to be January to September (Kelley and Shaw, 1943; Kelley, 1946), December to July (Underwood, Shier and Davenport, 1944) and from February to August or September in fine-wool Merinos at Armidale N.S.W. (Barrett, Reardon and Lambourne, 1962).

Riches and Watson (1954) in an experiment conducted at Cunnamulla using 'station ewes' joined with 'Peppin Merino' rams found that there was a definite breeding period from December to July. There were, however, about 20% of ewes that exhibited oestrus during each month over the period August to November. These results contrast with those of Kelley and Shaw (1943) who observed similar sheep at the same site and found that there were quite long periods of complete anoestrus.

An explanation for the difference may be that Kelley and Shaw did not introduce fresh ewes to the ewes that were continuously in the presence of rams, as in the case of Riches and Watson. Barrett *et al.* (1962) have suggested that the presence of freshly introduced ewes being served by vasectomised rams may have a stimulating effect on the 'continuous' ewes to exhibit oestrus. Alternatively, the introduction of fresh ewes may stimulate the rams, by increasing their libido and/or sensitivity in detecting oestrus, to such a degree that they are able and/or willing to detect and mount 'continuous' ewes.

(ii) Suddenly associated with rams

The breeding season of Merino ewes that are kept separate from rams prior to the time of joining has been shown to begin earlier (Barrett *et al.*, 1962; Lishman and Hunter, 1967) and continue later (Riches and Watson, 1954) than that of ewes run continuously in the presence of vasectomised rams. In several instances breeding has been found to occur throughout the year (Riches and Watson, 1954; Lishman, 1969).

(iii) Separated from rams

In ewes completely separated from rams the annual onset of oestrus may be even later than for ewes continuously in the presence of rams (Radford and Watson, 1957). Lishman and Hunter (1967) observed that Dohne Merinos continuously associated with rams tended to continue oestrous cycles, but in the absence of rams these ewes tended to stop oestrous activity until they were stimulated by the introduction of rams.

Differences between strains of Merinos in the timing of the annual onset of oestrus could arise from being bred at a particular time of year over many generations (Kelley and Shaw, 1943; Barrett *et al.*, 1962).

(b) Synchronisation of oestrus

Ewes joined in late spring or early summer show a marked synchronisation of oestrus some 14 to 20 days after joining (Underwood *et al.*, 1944; Thompson and Schnickel, 1952; Schinckel, 1954a; Riches and Watson, 1954).

Schinckel (1954), in studies conducted at Roseworthy College in South Australia, showed that during the transition period from the non-breeding to the breeding season, the primary effect of the sudden presence of rams was to stimulate ovulation without oestrus in the majority of those ewes not already exhibiting cyclic breeding activity. He conlcuded that stimulation occurred within six days of the rams being joined and speculated that, had the ewes not been slaughtered, they would have exhibited behavioural oestrus associated with ovulation one oestrous cycle later. Radford and Watson (1957), taking the appearance in the vagina of opaque white to cream-coloured semi-solid material of cheesy consistency to indicate ovarian activity of the type leading up to and associated with ovulation (Radford and Watson, 1955), showed that Schinckel's speculation was correct. Lyle and Hunter (1965) and Hunter and Lishman (1967) have both reported similar conclusions from South African studies of Corriedale and German Merino ewes, respectively.

It seems that the level of oestrous activity is most responsive to ram stimulation at the time when oestrus is beginning to re-appear in the flock after the annual anoestrous period (Radford and Watson, 1957; Watson, 1961). The timing and level of this behaviour varies from year to year (Watson and Radford, 1960). The presence of rams can have an effect at times other than at the transition from the non-breeding to breeding season (Lishman, 1969; Bellinger and Mendel, 1974) but in some circumstances this effect may not be of sufficient intensity to result in overt oestrus (Bellinger and Mendel, 1974).

The sudden introduction of rams to ewe flocks of two tropical breeds of sheep (West African Dwarf and Nungua Black Head), that are thought to ovulate and cycle throughout the year, has been reported to cause a synchronisation of oestrus. However, unlike temperate breeds, these animals exhibited oestrus and ovulated (as shown by subsequent lambing) within several days of the rams being introduced (Ngere and Dzakuma, 1974).

The stimulation provided by the sudden introduction of rams declines over two or three months (Lishman, 1969; Oldham, 1978). After that length of association the incidence of detected oestrus is generally similar to that in ewes completely separated from rams, although several reports (Lishman and Hunter, 1967; Lishman, 1969) suggest that the continuing presence of rams will delay the onset of anoestrus. Lishman (1975) found that anoestrous ewes that had been continuously associated with rams had a reduced sensitivity to oestrogen compared with those that had been isolated from rams for three months. He concluded that ewes subjected to mating stimulus for several months become less sensitive to stimuli which induce overt oestrus. However, it is not clear from his paper whether the ewes selected were equivalent. While there was an equal number of ewes in each group, and they were selected from equal sized groups, the 'isolated' ewes were selected at random but the 'associated' ewes were selected from only those ewes that were anoestrus. It seems possible that the higher sensitivity among the isolated ewes might have resulted from them not all being anoestrus.

(c) Nature of synchronisation effect

The stimulating effect of rams does not require direct contact of ewes and rams; smell and sound of rams in an adjoining yard will provide the stimulus, but rams kept one hundred yards (91 metres) or more from the ewes do not (Watson and Radford, 1960). Watson and Radford were not able to determine if smell alone or sound alone provided the stimulus. Nor did they investigate the effect of sight.

More recent work (Morgan, Arnold and Lindsay, 1972) in Western Australia has shown that a high proportion of Border Leicester x Merino ewes with their sense of smell impaired were not stimulated to exhibit oestrus during November and December, whereas ewes with the senses of touch and/or hearing impaired and intact ewes were nearly all detected in oestrus. The authors concluded that rams stimulate oestrous activity in non-cycling ewes through olfactory receptors in the ewes. They did not specifically test the sense of sight.

Chesworth and Tait (1974) found that there was a sudden rise in the plasma luteinizing hormone (LH) level of Border Leicester x Scottish Blackface yearling ewes about 8 to 12 hours after being joined with rams. The LH peak, however, was small (mean 2.3 ng/ml) compared with that for normally cycling ewes at the time of oestrus (up to 28 ng/ml). The authors suggested that these circumstances may well explain why the presence of rams affects ewes that are near the expected end of anoestrus, but have not cycled, but has no influence on those that have started to cycle. Their finding and view is consistent with the more general views of Hafez (1952) and Watson (1952). Hafez suggested that the onset of ovarian activity and the onset of the breeding season require two different levels of pituitary activity; a lower level that causes ovulation and a higher one that is necessary for the manifestation of oestrus. He postulated that there was a seasonal cycle in pituitary activity that was inverse to daylength and also that differences in the length of the breeding season, between breeds, could be explained by particular breeds requiring a relatively high or low pituitary activity to initiate ovulation or oestrus. Those breeds requiring a high proportion of their maximum level would have a short breeding season while those requiring a low proportion would have a long season. Watson (1952), after assessing many measures of sexual activity, concluded that the evidence supported the concept of an annual rhythm in which the activity increases gradually from a low level to a high level and then falls gradually to a low level again. These three reports (Hafez, 1952; Watson, 1952; Chesworth and Tait, 1974) suggest that a relatively small stimulus, such as that given by the sudden introduction of rams, may be sufficient to cause oestrus in ewes with pituitary activity only a little below their required threshold level, as for example might be expected in ewes either soon after becoming, or shortly before ceasing to be, anoestrous. The same stimulus applied to ewes that are deeper in anoestrus may not increase the activity above the threshold level.

4. OESTRUS AND NUTRITIONAL STATUS

The effects of level of nutrition, and subsequent changes in body condition and liveweight, on the occurrence of oestrus have not been clearly defined. Under certain conditions there can be effects of current nutrition on the incidence of oestrous activity during the breeding season and also on the length of the breeding season. There is also evidence of a long term effect in which low nutrition in previous seasons depresses oestrous activity even after the animals have regained their lost liveweight.

Low levels of nutrition during the breeding season have been found to reduce the incidence of oestrous activity during the season.

Hafez (1952) working at Cambridge, subjected Suffolk ewes to severe undernutrition such that they lost, on average, 45% of their initial liveweight (about 32 kg) over 14 weeks. This treatment, beginning soon after the onset of the breeding season, resulted in a 34% incidence of silent heats during the breeding season (expressed as a percentage of the total number of cycles possible). There were no instances of silent heat in the control animals fed a maintenance diet. Allen and Lamming (1961), working at Nottingham, found that Kerry Hill ewes fed to lose 9.5 kg (about 17%) over 12 weeks also had a high incidence of silent heats. MacKenzie and Edey (1975) reported a similar response in Merino ewes. These workers also reported that a seven day fast (during which the ewes lost about 15% of their weight) suppressed oestrus by 30% even though the ewes were of high body weight.

Low nutrition during the breeding season can also hasten the cessation of oestrous activity. McKenzie and Terrill (1937), working in Missouri, U.S.A., with 3-year-old Rambouillet ewes fed in a dry-lot either to gain 6.4kg (about 14% of bodyweight) or lose 4.5kg (about 10% of bodyweight) between October 7 and February 24 found the average end of the breeding season to be February 4 and December 18 respectively. Peppin Merinos observed at Brisbane, Queensland, showed an abrupt decrease in sexual activity when changed to a low level of nutrition towards the end of their breeding season (Smith, 1962). Merino ewes fed in a dry lot in eastern Transvaal, South Africa, were found to have a reduced sexual season when placed on a restricted ration about one month after the onset of the breeding season (Roux, 1936). A similar effect has also been reported for mature-age Merino ewes in South Africa by Hunter (1961). He found that ewes fed a low ration from early in the breeding season had a shorter breeding season than ewes well fed throughout the year.

However, in contrast to Smith (1962), ewes fed a submaintenance diet beginning late in the breeding season did not show a shortened breeding season but behaved in a similar manner to the ewes well fed throughout the year. It seems that while low nutrition applied during a major portion of the breeding season will reliably hasten the cessation of oestrous activity, the effect of its application late in the season is variable.

Smith (1966a) collated a number of reports from both South Africa and Australia and examined the relationship between seasonal environmental differences in pastoral conditions and the duration of anoestrus in Merino ewes (anoestrus defined as the period during which less than 50% of ewes exhibited oestrus). He found that when there were good feed conditions throughout the year there was no anoestrous period, but when there were poor fed conditions during either spring and early summer, summer and autumn or during winter there was, almost always, a period of sexual inactivity. Poor feed in winter was often associated with an anoestrous period that extended about a month longer into the summer months than that following poor feed in summer and autumn. This is in agreement with Quinlan and Mare (1931) who reported that in South Africa practical experience has taught farmers that the anoestrous period will be extended in years of drought.

This effect of seasonal nutritional conditions on the onset of anoestrus may result from the nutritional level experienced either during the current season or during a previous season. Smith (1966b) found that spontaneous oestrous activity in the first 17 days of joining was stimulated in Peppin Merino ewes fed an improved diet for three weeks before, and during the joining period. Experiments in both South Africa

(29°S) (Hunter, 1961, 1962) and Queensland (25°S) (Smith, 1962, 1966a, 1966b) indicate that the level of nutrition in a previous season can have a delayed effect on the current level of oestrous activity. Both authors found that activity in autumn was influenced by the level of nutrition during the preceding spring even though the liveweight difference had disappeared. Ewes maintained in good condition during the winter following treatment may still show an effect of the treatment in the following summer (i.e. a year later) (Smith, 1966b), but it is most likely that the effect will be overshadowed in magnitude by the level of nutrition experienced during the winter or spring. Fletcher (1974) was not able to demonstrate an effect of nutrition from the previous season among Merino ewes in South Australia.

5. OESTRUS AND BODY SIZE

While body size has been recognised as a component of liveweight (Edey, 1968; Williams, Thwaites and Fogarty, 1974), there has been scant attention paid to a quantitative relationship between it and the occurrence of either oestrus or ovulation. This is, presumably, because of the relatively tedious nature of the measurement process compared with that of either weighing, or scoring ewes for body condition - particularly in the context of a commercial application.

Williams *et al.* (1974) have investigated the effect of body size (measured by the method of Turner, Hayman, Riches, Roberts and Wilson, 1953) on the onset of the breeding season of Border Leicester ewes at two sites in New South Wales. While they were unable to detect either significant or consistent correlations the majority of correlations were negative, i.e. large animals came into oestrus earlier. Ducker and Boyd (1977) working at Glasgow (56°N) studied groups of Greyface ewes (Border Leicester rams over Scottish Blackface ewes) formed on the basis of ewe body size (after Turner *et al.*, 1953). There was no difference in the mean date of onset of oestrus among a group of 50 large ewes (calculated body size ranging from 60,000 to 80,000 cc) and a group of 50 small ewes (40,000 to 55,000 cc) both of equal average body condition.

6. OESTRUS AMONG KOONOONA STRAIN MERINO EWES

Seasonal variations in the occurrence of oestrus has recently been studied over a one-year period (Cutten, unpublished). The pattern of oestrus, as detected by freshly introduced entire rams, was observed at each of eight periods spread evenly between March 1970 and February 1971. Each of the eight groups were joined at a mean liveweight of about 49kg: the natural seasonal variation in liveweight having been deliberately controlled.

On each occasion almost all of the ewes were detected in oestrus within 35 days after the rams were introduced. In contrast, the pattern of occurrence of oestrus varied with the season of joining. During summer almost all of the ewes were detected in oestrus during the first 14 days following joining. However, as few as 25% of the ewes in the flocks joined during late winter and early spring exhibited oestrus during the first 14 days. On these occasions there was a marked synchronisation of oestrus during the second fortnight of joining.

The oestrous activity of ewes "descended, for upwards of fifty years, from rams purchased from 'Kanoona' and 'North Bungaree'", but "bred and reared on the Monaro, in the south-east of New South Wales" was studied between May 1937 and December 1941 (Kelley and Shaw, 1943). Three flocks of ewes were maintainted; one in the south-west of Queensland, one west of Sydney, and one at Cressy in Tasmania. The ewes were run with vasectomised rams throughout the period of observation. At each site the proportion of the flock detected in oestrus each month varied with the season of the year. All, or most, of the ewes were detected in oestrus during autumn while few, or none, were detected during spring and early summer. There was year to year variation in the season of onset, and in the intensity of oestrous activity, at each site. Despite a 13° spread in latitude there was not a consistent effect of site. On this basis a similar performance would be expected at Turretfield.

It is apparent that Koonoona ewes experience a definite anoestrous period either when they are isolated from rams or are continuously associated with them. Data derived from observations throughout a year show that a sudden association with rams will provide sufficient stimulus to cause behavioural oestrus even during the season of deepest anoestrus.

The oestrous behaviour following the introduction of rams is of potential interest to commercial sheep farmers who wish to join their flocks during winter or early spring. It appears that the oestrous performance of a flock of Koonoona ewes would not be impaired by a management decision that involved changing the time of joining to these seasons. However, before such a decision could be taken with confidence the behaviour would need to be observed in at least one more year and at several different liveweight levels. Both of these factors are considered in the present study.

OVULATION

B. THE EFFECT OF NUTRITIONAL STATUS, SEASON AND BODY SIZE ON OVULATION IN EWES

1. INTRODUCTION

The ovulation rate of ewes is known to be influenced by the breed, age and nutritional status of the ewes and by environmental factors. While it is not within the scope of this study to consider the effects of breed or age it can be said that, in general, ewes of different breeds or age respond to changes in the latter two factors in a similar manner, but the level of response to any given change may be different. Under natural conditions the latter two factors are subject to seasonal variation and it follows that the level of ovulation is also season dependent.

In attempting to elucidate the relationship between ovulation, nutritional status, environmental factors and season most studies have been made of the relation between one of several measures of nutritional status and ovulation. For these studies workers have used either liveweight, or body condition (one of the components of liveweight), as the measure of nutritional status and most have compared groups of ewes with different mean nutritional status under the same seasonal and environmental conditions. Fewer studies have been made of the comparison of ovulation at several different levels of nutritional status at several seasons, of ovulation at constant nutritional status throughout the year or of interactions between nutritional status and season.

Liveweight can be considered as having two components, namely, body size and body condition. While as stated previously, the relationships between ovulation and both liveweight and body condition have been studied there has been little attention given to determining possible relationships between ovulation and body size.

2. OVULATION AND NUTRITIONAL STATUS

(a) Introduction

It has long been recognised that the lambing performance (as distinct from mean ovulation rate) of a flock of ewes can be improved by increasing the level of nutrition for a short time before mating. The early literature on this effect, which had loosely been termed "flushing", has been reviewed by Moule (1962).

In considering the literature since before the turn of the century, Moule found that reports often conflicted about the nature of the effect. He considered this not surprising, as many of the reports were based on survey results of farmer opinion with no (or little) regard for detail such as liveweight, body condition or age of the ewes. In addition there was not a clearly accepted definition of the meaning of the term flushing. Some authors considered it to be a procedure for ensuring that ewes were in a good, strong, well-fed state at mating, while others considered it to mean a state of rapidly increasing body condition at mating.

In the late 1950's the practice of flushing was regarded as one of providing ewes in fairly poor condition with an improved level of nutrition for several weeks before joining so that they were rapidly rising in condition when mated: providing extra feed for ewes already in good condition was not regarded as flushing. This practice was considered to enhance reproductive performance and was being applied commercially. In fact a number of New Zealand prime lamb producers adopted the practice of confining ewes onto bare pastures after weaning "in order to keep the condition off them so they will respond to flushing" (Coop, 1962).

Moule (1962) noted that investigators, with a few exceptions who used factorial designs (Darroch, Nordskag and Van Horn, 1950; Allen and Lamming, 1961), had failed to explore the possible separate effects of level of nutrition prior to mating and liveweight (or body condition) at mating on the subsequent reproductive performance. Prior to the early 1960's only a few workers obtained information about ovulation rates and thereby avoided the confounding effects of reproductive failure, in the post-ovulatory to pre-natal period, on their interpretations of lambing performance data (McKenzie and Terrill, 1937; Allen and Lamming, 1961; Wallace, 1961). The investigations of Allen and Lamming (1961) appear to be the first to have included nutrition treatments in a factorial design and also to have measured ovulation rate.

Since that time there has been a number of intensive studies of the relationships between ovulation and both liveweight at, and liveweight change before, mating. There has been a smaller number of studies of the relationship between ovulation and body condition.

(b) Liveweight

The effects of liveweight at ovulation (or mating) or liveweight change prior to ovulation (or mating) on ovulation rate (or lambing performance) have been examined in a number of experiments and the separate nature of these effects has been established.

(i) Liveweight at ovulation

Wallace (1958) reported the lambing performance of a flock over a number of years and noted that it followed closely the mean liveweight of the ewes at joining. He subsequently conducted an experiment, repeated over two years, in which Romney ewes were grazed for two months at either high, medium or low levels of nutrition and then recombined as a single flock for three weeks before, and during, joining (Wallace, 1961). There was a substantial positive association of liveweight at joining with both the number of lambs born per ewe lambing and the number of ewes joined that subsequently lambed. A similar relationship between liveweight at joining and lambing performance was found by Tribe and Seebeck (1962) in Border Leicester x Merino ewes.

Coop (1962) working at Canterbury (New Zealand), investigated the breeding performance of a large number of ewes, mainly Corriedale, over a 15 year period and found a considerable influence of liveweight at joining on reproductive rate. The incidence of twin births increased by about 6 per cent for each 4.5 kg (10 lb) increase in mean liveweight over the range 41 to 64 kg (90 to 140 lb). The incidence of barren ewes was relatively independent of liveweight above 41 kg (90 lb) but increased rapidly below that weight. While these relationships were determined from a study of between-flock variation, Coop was also able to examine the data for some of the ewes on a within-flock basis. He concluded that the within-flock relationship was "not very dissimilar" to the between-flock one.

There have been several reports since that are in general agreement with these findings (Coop, 1966a; Killeen, 1967; Suiter and Fels, 1971). McInnes and Smith (1966) however, did not find an association between bodyweight at conception and the number of twin births. They pointed out that this apparent inconsistency may be due to the relatively small numbers in each treatment group (about 20), to the history of low fecundity in the ewes (based on previous years) and to the known low fecundity of the particular strain of ewe when mated in the spring (as in their experiment).

A relationship similar in nature, but of greater magnitude, to that found by Coop (1962) between liveweight at mating and the incidence of twin births has been found between liveweight at mating and ovulation rate in Border Leicester x Merino crossbred ewes (Killeen, 1967), in Peppin Merino ewes (Edey, 1968), and in South Australian strong wool Merino ewes (Fletcher, 1971). The difference in magnitude reflects the expected losses due to failure of fertilization and to embryonic and neonatal deaths.

Edey (1968) considered the nature of the relationship between liveweight and ovulation rate over a wide range of liveweight using pooled data collected during the course of 11 experiments (designed primarily to study embryo mortality). Ewes for these experiments were purchased through local saleyards and were not a uniform flock, although all were Peppin Merinos of mature age. In all experiments bodyweight was stable at the time of ovulation (April or May of four consecutive years). Ewes were either run at pasture (8 experiments) or hand fed in pens (3 experiments). Analysis of these data, covering the bodyweight range from less than 30 kg to greater than 55 kg, showed that ovulation rate was fairly uniform below 37.5 kg and then increased rapidly before apparently reaching a plateau at about 55 kg. This finding, derived from a heterogeneous sample of Merino ewes, is not necessarily related entirely to the effects of level of nutrition. It could be, and almost certainly is, confounded with ewe frame size and/or different genetic potential for ova production.

Observations on South Australian strong-wool Merino ewes have shown that liveweight at ovulation is positively associated with the incidence of twin ovulation (Fletcher, 1971). A significant linear relationship was found over the liveweight range of 42 to 55 kg with the incidence of twin ovulation increasing by about 2.5 per cent for each 1 kg increase in liveweight at ovulation.

(ii) Liveweight change shortly preceding ovulation

Coop (1962) concluded that the classical concept of flushing must be modified to one in which the actual body condition, or liveweight, of the sheep at ovulation and the dynamic rising condition leading up to ovulation are both of considerable significance. He referred to these two effects as "static" and "dynamic" and has defined them (Coop, 1966b) as

(a) Static effect - the level of liveweight at ovulation brought about by flushing. This is not specifically related in time to mating. An increase in liveweight brought about at any time of the year if maintained until mating will cause a higher lambing percentage.

(b) Dynamic effect - the effect of the dynamic process of change in liveweight or condition leading up to, and including the time of mating (ovulation).

Since Coop's publication in 1962 work has been directed towards elucidating the extent of the static and dynamic effects produced by providing ewes, in a range of body condition, with high levels of nutrition for a short period before joining.

The first major study reported is that by Coop (1966a) who conducted a series of experiments designed to determine whether there was a true flushing effect resulting from changing liveweight as distinct from any effect produced by a gain in liveweight, and if so, to measure the relative magnitude of the separate responses. These experiments, using Border Leicester x Romney, or Border Leicester x Correidale crossbred ewes of mixed age showed that there was a dynamic flushing effect, separate from, and independent of, the static liveweight effect. Under the severe experimental conditions imposed a period of six weeks flushing increased the lamb drop by 12 per cent: under more realistic farm practice Coop suggested the effect would probably be 6-8 per cent. Flushing for one oestrous cycle increased the drop by 5-6 per cent while flushing for half an oestrous cycle produced no detectable response.

Killeen (1967) found a similar independent dynamic effect on the incidence of multiple ovulation in Border Leicester x Merino ewes. McInnes and Smith (1966) considered the effect of their flushing treatments on Peppin Merino ewes to be entirely dynamic - they were unable to demonstrate a static effect. Fletcher (1971), on the other hand, concluded that there was no dynamic effect of flushing among South Australian strong-wool Merino ewes and that the incidence of multiple ovulation was related entirely to liveweight at ovulation.

It is of interest to review the results of a number of flushing experiments in the light of there being separate static and dynamic effects of liveweight. Assuming that there is an increased incidence of about 6 per cent in multiple births, and 10 per cent in multiple ovulations, for each 4.5 kg (10 lb) increase in mean liveweight then it follows that the increased liveweight produced by flushing can account for most (Underwood and Shier, 1941; Fletcher, 1971), some (Wallace, 1951, 1953; Tribe and Seebeck, 1962; Coop, 1966; Killeen, 1967) or very little (Darrock *et al*., 1950; Allen and Lamming, 1961; McInnes and Smith, 1966) of the observed response. This situation clearly suggests that the present understanding of the so-called static and dynamic effects of liveweight is inadequate to consistently explain the observed ovulation rate.

In some circumstances undernutrition may not affect ovulation despite a decrease in liveweight. Short term undernutrition (water but not feed available for seven days) prior to ovulation has been found to have no effect on the ovulation rate of Merino ewes in good condition, although the number of follicles present 2-3 days after ovulation was reduced (Mackenzie and Edey, 1975). Allen and Lamming (1961) found that despite an 11 per cent decrease in liveweight the ovulation rate of ewes in good condition did not decrease until more than four weeks after they were subjected to a submaintenance diet. On the other hand, while Fletcher (1971) found that ewes reduced from high to medium liveweight over five weeks had a similar ovulation rate to ewes maintained at the medium liveweight, ewes reduced from medium to low liveweight over the same period had a higher ovulation rate than ewes maintained at the low liveweight. Fletcher suggested that at decreasing low liveweight the level of ovulation is better associated with the liveweight of several weeks before ovulation. However, Farrell and Reardon (1972) found that sheep maintained at low liveweight had a greater proportion of water, and a smaller proportion of protein, in their fat-free empty body than normal. Thus an alternative explanation, to that given by Fletcher, could be that the group maintained at low liveweight had a higher proportion of water and therefore the "effective liveweight" in terms of ovulation was less than the actual liveweight, i.e. the liveweight was artificially high due to increased water content. This explanation assumes that ovulatory activity is related to body components other than water, and implies that the ovulation-liveweight relationship is not linear at low liveweight.

(iii) Liveweight in preceding seasons

Severe undernutrition of South Australian strong-wool Merino ewes resulting in low liveweight during autumn and winter of one year has been shown to depress their ovulation rate in the following summer relative to ewes maintained in either moderate or good condition (Fletcher, 1974). This occurred even though all three groups of ewes had similar mean liveweights at the time ovulation was measured.

(c) Body condition

Most investigations of the nature of flushing have attempted to relate ovulation rate or lambing performance to liveweight. Liveweight, however, is a function of body size (frame size), body condition and gut-fill and some investigators have examined possible relationship between various measures of body condition and reproductive performance.

A major problem of investigations involving body condition is that of finding a measure of condition that can be applied quickly over a large number of animals. For example while Tribe and Seebeck (1962) considered that body condition could be a more useful indicator of reproductive performance than liveweight they stated that they were unable to study this aspect because there was, at that time, no satisfactory objective technique for assessing "condition" of sheep. Presumably they were not prepared to use a subjective condition score based on that used by McClymont and Lambourne (1958).

Russell, Doney and Gunn (1969) developed a subjective score based on that described by Jeffries (1961) and found that their, "agreed value" score provided a more accurate estimate of total body fat than did liveweight. This technique provides an estimate of total body fat in live sheep of equal accuracy to that obtained either by direct measurement of back fat thickness or by the use of an objective body condition index based on the weight/size ratio of the animal (Guerra *et al.*, 1972a).

(i) Body condition at ovulation

Gunn *et al.* (1969) used their condition score (Russel *et al.*, 1969) to arrange Scottish Blackface ewes into groups of different body condition score. They found that there was a significant relationship between body condition and ovulation rate with ewes in condition 3 (moderately fat - estimated 29% chemical fat) having a mean ovulation rate of 2.07 while for those in condition 1.5 (fairly lean - estimated 16% chemical fat) the rate was 1.15. Later work (Gunn, Doney and Russel, 1972) showed a relationship of a similar nature but highlighted the effect "different flocks" can have on the magnitude of the response.

Bastiman (1972) found a relationship between body condition at mating and lambing performance. He pointed out that meaningful predications of lambing performance could only be made when applied on a group basis as there was considerable variation in individual performance among ewes of any given condition score. He also concluded that a better prediction of lambing performance could be obtained by grouping ewes on the basis of body condition than on liveweight. This is in contrast to McInnes and Smith (1966) who concluded that body condition offered no real advantage over liveweight. It should be noted, however, that they used a different scoring system - that of McClymont and Lambourne (1958) - and that the observations were made under conditions of gaining liveweight and body condition, induced by short term flushing.

(ii) Body condition change preceding ovulation

The effect on ovulation rate of changing levels of body condition immediately prior to mating have been studied. Gunn, Doney and Russel (1969) found no effect of either an increasing or decreasing body condition in comparison to a steady state when Scottish Blackface ewes were mated at a common condition score of 3. However, at condition score of 1.5 the result was not clear-cut. On the basis of a trend, the results could have been interpreted as suggesting that when ewes are in poor condition at mating, ovulation rate may be positively related to the level of nutrition prior to mating. However, later work (Gunn and Doney, 1975) did not substantiate this view and they then concluded that, in respect of ovulation rate, there was no interaction between the level of nutrition shortly before mating and the level of body condition at mating, at the condition levels studied. The findings in relation to body condition score 3 have been confirmed by Gunn and Doney (1975) and also, after a longer period of maintenance, by Gunn and Doney (1973). In the latter experiment the lambing performance of ewes recovering condition (condition score 2 to 3) quickly after their lambs were weaned and then maintaining condition for two months before mating was similar to that of ewes recovering condition in 5 to 8 weeks immediately prior to mating.

3. OVULATION AND SEASON

Under normal grazing conditions the liveweight and body condition of ewes will vary from season to season as a result of cyclic changes in both the quantity and quality of feed available. Thus, because of the established effects of both liveweight and body condition on ovulation, it is to be expected that ovulation rate will also be subject to seasonal fluctuation (seasonal variation), as indeed numerous experiments have shown (e.g. McKenzie and Terrill, 1937; Watson, 1952; Averill, 1959; Restall, Fowler and Brydon, 1965). Even before these relationships had been enunciated, however, Watson (1952) concluded that not all of the seasonal variation could be explained on the basis of differing nutritional conditions and suggested that seasonal changes in physical factors of the environment may have an influence.

Clear evidence for the existence of an effect of season, separate from either liveweight or body condition, was first provided by Radford (1959) who maintained ewes at a constant liveweight (on a wool-free basis) throughout a whole year. He found, by repeated observations on the same ewes, that there was significant variation throughout the year in the ratio of twin to single ovulations (incidence of twin ovulation). The incidence of twin ovulation observed in these medium-wool Merino ewes housed in open-sided, partly roofed, concrete pens at Melbourne, was low in November (23 and 38% of ewes ovulating in consecutive years), high in March - May (82 and 78%) and intermediate in both August (59 and 57%) and January (43%). Seasonal variation in ovulation rate has also been observed in aged Rambouillet ewes fed in a dry lot at McGregory in Texas

(Shelton and Morrow, 1965). These ewes, which were at a similar mean liveweight at each of the four seasons at which observations were made, exhibited their lowest mean ovulation rate (1.06) in March (spring) and their highest (1.75) in September (autumn).

A cyclic pattern of seasonal variation in the incidence of twin ovulation has also been observed in South Australian strong-wool Merinos run in small open yards (Cutten, unpublished). However, the magnitude was smaller, and the phase some two months earlier, than reported by Radford (1958) with the lowest incidence being 10-15 per cent in August - September and the highest 35-40 per cent in January - March. The peak incidence is in agreement with that reported by Fletcher (1971), who, using animals with the same mean liveweight and from the same flock found an incidence of 32 per cent in January and 26 per cent in April.

There do not appear to be any reports of experiments investigating seasonal variation in ovulation rate at constant body condition.

The most likely physical environmental modulators of ovulation rate are daylength and temperature (Radford, 1958). Evidence of a substantial effect of daylength is provided by Ducker and Boyd (1974) who found that ewes responding to an abrupt decrease in artificial daylength can have ovulation rates as high as that measured in ewes during the peak of their natural breeding season. The fact that these ewes responded three months earlier than normal indicates that any effect of seasonal change in temperature is unimportant relative to that of the change in daylength.

4. OVULATION AND FEED QUALITY

The importance of the quality of the diet of ewes immediately prior to, and during, mating to their subsequent lambing performance has not been studied in detail until recently. While Bellows, Pope, Meyer, Chapman and Casida (1963) suggested that the amount of protein in the body may influence ovarian activity it was generally accepted that energy, not protein, was the important component of the diet involved in flushing. For example, Coop (1966b) considered that "there is no evidence that there is any specific feed factor such as high protein content which is conducive to flushing".

The work of Memon, Antoniewicz, Benevenga, Pope and Casida (1969) seems to have been the first to examine the ovarian activity of ewes fed at different levels of protein (272 and 68 g digestible protein/day) at each of two levels of energy intake (21.8 and 13.4 MJ digestible energy/day). The results of these treatments, applied for about 8 weeks before ovulation, indicated that ovulation rate was significantly increased by the higher energy diet at both levels of protein but that there was no effect of protein level at either level of energy. It should be noted however, that while the authors made no comment, the data suggest that there could be a response to protein at the lower level of energy. Torrell, Hume and Weir (1972a) provide evidence, from pen, experiments, that protein level of the diet influences lambing percentage. In these experiments they provided diets with various energy and protein levels by feeding differing amounts of lucerne wafer and rolled barley grain. In the first experiment the number of lambs born per 100 ewes present at lambing (lambing percentage) increased from 102 per cent for ewes receiving 33 g N and 8.4 MJ DE/day to 166 per cent for those receiving 53 g N and 18.4 MJ DE/day. In a second experiment, designed to provide a lower range of protein levels, lambing percentage increased from 107 per cent for ewes receiving 10 g N and 8.0 MJ DE/day to 139 per cent for those receiving 46 g N and 19.3 MJ DE/day.

Multiple regression analysis of the data from the first experiment showed that 72 per cent (62% in the second experiment) of the total variation was accounted for by the regression and that of this the amounts due to protein, energy, and protein and energy combined were 7 per cent, 61 per cent and 32 per cent respectively (21%, 35% and 44% in the second experiment). The authors suggested that the greater effect of protein in the second experiment could have been due, at least in part, to the lower level of protein fed as the basal treatment (10 g N/day compared to 33 g N/day).

Ovulation rate responses to the quality of the feed have also been shown in field experiments (Torrell, Hume and Weir, 1972b; Lightfoot and Marshall, 1974; Knight, Oldham and Lindsay, 1975). Torrell, Hume and Weir (1972b) conducted an experiment over four years at Davis, California, in which ewes grazing dry range pasture (annual grasses mainly *Bromus* spp., annual forbs and some subterranean clover) were compared with similar ewes either supplemented for 17 days prior to and for the first 17 days of joining, fed in a drylot or grazed on improved pasture over the same period. Supplementation (2.25 kg lucerne pellets/ewe/week, fed twice weekly) did not improve lambing performance, but drylot feeding of 1.82 kg lucerne hay/ewe/day increased the number of lambs born/ewe present at lambing from 101 to 128 per cent, while access to improved pasture also increased lambing percentage from

110 to 138 per cent. In most years all groups lost weight over the experimental period but the supplemented and improved pasture groups lost least. Lambing performance (lambs born/ewe present at lambing) was not related to the initial liveweight of the ewes but was strongly related to liveweight change during the 34 day treatment period with an increase of about 8 per cent for each kg increase in liveweight. Blood urea nitrogen levels measured in plasma samples at the day of joining were higher for ewes fed in the drylot or grazing improved pasture than for the other two groups.

In Western Australia, ewes grazing dry subterranean clover pasture (moderate level of crude protein) had a higher mean ovulation rate than similar ewes grazing cereal stubble (relatively low level of crude protein) (Lightooft and Marshall, 1974). Ewes grazing on stubble and provided with a lupin grain supplement (relatively high level of crude protein) had an even higher ovulation rate (Lightfoot and Marshall, 1974; Knight, Oldham and Lindsay, 1975).

The nature of the ovulation response to lupin grain has been examined in relation to both the rate (Lightfoot and Marshall, 1974), and duration of supplementation (Marshall and Lightfoot, 1974; Lindsay, 1976). Lightfoot and Marshall found ovulation rate to be quantitatively related to the daily intake of grain with increases from 1.25 to 1.61 on subterranean clover pasture and from 1.17 to 1.50 on wheat stubble as supplementation increased from 125 to 500 g/ewe/day. The small differences in mean liveweight (2-3 kg) generated by the different levels of supplementation are insufficient to account for the response in terms of the generally accepted levels of static and dynamic liveweight effects on ovulation rate (Fletcher, 1971).

Marshall and Lightfoot (1974) investigated the duration of supplementation necessary and found that feeding for either 14 or 35 days, prejoining (together with the first 18 days of joining) resulted in a similar level of response in ovulation rate. More recently the response has been shown to occur as early as about 6 days after the beginning of supplementation and to cease within several days of its discontinuance (Lindsay, 1976). This rapid response in ovulation rate occurs too quickly, of course, for the ewes to experience a significant change in liveweight, and is most definitely in contrast to the static and dynamic theories of liveweight effect. Foote *et al.* (1959) have also reported a response in ovulation rate to short term changes in nutrition unaccompanied by an appreciable liveweight change: in this case a supplement of "grain mixture" comprising 5 parts of cracked shelled corn; 3 parts whole oat; 1 part linseed meal and 1 part of wheat bran.

It is evident, therefore, that sudden changes in the quality of the feed available to the ewes can affect their reproductive performance in a manner unrelated to, or at least unassessable by, changes in liveweight. Lindsay (1976) suggested that the ovulation rate in ewes is related to their "net nutritional status", i.e. the sum of endogenous katabolic sources of nutrients and uptake of exogenous nutrients from the gut. Thus heavy ewes given poor feed may still produce a reasonable number of twin ovulations because they have a considerable endogenous source of energy and protein. On the other hand, poor ewes temporarily well fed will also ovulate well because of the contribution of the exogenous source of nutrients to their "net nutritional status".

5. OVULATION AND BODY SIZE

At the time this study was organised there were, to the author's knowledge, no reports relating body size directly to ovulation rate, either in flocks held at a steady liveweight or in flocks experiencing liveweight change. However, ovulation rate had been found to be influenced, on a within flock basis, by "inherent variation in mature liveweight' in a manner that was independent of variation in liveweight due to recent nutrition (Fletcher, 1971). This effect, observed in Koonoona strain South Australian strong-wool ewes, obviously could have been related to inherent body size and/or to inherent body condition. Nichols and Whiteman (1966), working in south-west Texas, measured the lifetime productivity of Rambouillet/Panama ewes in relation to a measure of body size (average of a number of liveweights corrected to a constant body condition score). They concluded that there was little effect of body size. Larger ewes produced only slightly more kilograms of lamb and wool during their lifetime than did smaller ewes.

Since the beginning of the present study there have been reports relating ovulation and ewe body size. Guerra, Thwaites and Edey (1972b) worked at Armidale, New South Wales, with groups of Merino ewes chosen on the basis of their large or small body size. They found that big ewes experienced more multiple ovulations than small ewes and that there was a significant linear relationship between ovulation rate and body size. However, body size and ovulation were not significantly correlated when considered at constant body weight. The apparent body size/ovulation relationship resulted from big ewes, in terms of frame size, also having high body weight. They concluded that body weight at mating was a better predictor of ovulation rate than body size (or body condition). Ducker and Boyd (1977) conducted an experiment of similar overall design to that of Guerra *et al.* (1972b), but worked at Glasgow and used Greyface ewes. They found that the body size of their ewes had no effect upon ovulation rate. The large and small ewes were in an equal condition but the large ewes were, on average, 14 kg heavier than the small ewes. Ducker and Boyd suggested that the different in behaviour between their ewes and those of Guerra and co-workers may be related to the different levels of performance. The Merino ewes were of smaller body size and had a lower ovulation rate and a higher incidence of barrenness than the Greyface ewes.

Cumming (1977) reported an examination of 11 experiments conducted in Victoria. He found that the mean ovulation rate per ewe increased from 0 to 0.44 for each 10 kg increase in liveweight of ewes within a flock. In most instances the increase was between 0.25 and 0.30. The response was least when the flock liveweights were lowest and when ewes were studied either about the summer solstice or at the beginning of the breeding season. He also reported that liveweight alone was as accurate a predictor of ovulation rate as both liveweight and body condition score (palpated by the method of Russel, Doney and Gunn (1969)).

6. WITHIN-FLOCK RELATIONSHIPS

'Inherent liveweight' has been shown to influence the incidence of twin ovulations (Fletcher, 1971). These observations, in Koonoona strain Merino ewes, showed that the incidence increased by about 1.3 per cent for each 1 kg increase in inherent liveweight, or about half the rate of increase for liveweight change resulting from improved nutrition. Fletcher did not consider the relative effects of body size and body condition as components of the inherent liveweight effect.

Since then there have been several reported studies of the within flock relationship between body size and ovulation (Guerra, Thwaites and Edey, 1972b; Ducker and Boyd, 1977). Guerra *et al.* (1972b) found that the incidence of multiple ovulations was greater among big ewes than among small ewes. They also grouped the data into body size classes and found that there was a significant regression with ovulation increasing by 3 per cent for each 1,000 cc increase in size. This regression analysis may have confounded some nutritional effects with body size. Ducker and Boyd (1977) did not calculate regressions but compared groups of ewes selected for either large or small body size. As mentioned in Section 5 above they found no effect of body size.

Macfarlane, Dolling and Howard (1966) found that high wool producing Merino ewes also had high water turnover compared with that of low wool producing animals from the same flock. As the higher wool production may correlate with total energy turnover it is possible that high water turnover could indicate high hormone production and, in particular, cause high ovulation rate. The possibility of a within-flock relationship between water turnover and ovulation is considered in the present study.

7. OVULATION AMONG KOONOONA STRAIN MERINO EWES

Several factors affecting ovulation in Koonoona strain Merino ewes have been investigated in pen experiments. It has been shown that the mean ovulation rate of ewes fed varying amounts of a hay and grain ration in small pens was related to their mean liveweight at ovulation, and that this relationship was not significantly affected by either an increasing or decreasing short term liveweight change immediately prior to ovulation (Fletcher, 1971).

While Fletcher (1971) was unable to detect any seasonal difference in ovulation rate between January and April in ewes of a given liveweight, Cutten (unpublished) found that ewes of similar liveweight (49 kg) joined at different seasons had mean ovulation rates that followed a generally cyclic pattern throughout the year. Ovulation rate ranged from 1.10 to 1.15 in August - September to 1.35 to 1.40 in January - March. In the light of this latter finding it is not surprising that Fletcher found no effect of season between January and April, rather, it indicates that Koonoona strain ewes have a period of several months in mid-summer and early autumn when season does not significantly affect their rate of ovulation. The ovulation rate in summer - autumn was similar in the two studies (Fletcher, 1971; Cutten, unpublished), and appears to be well established. However, the magnitude of annual variation in ovulation rate at constant liveweight requires further investigation as it has been determined in only one year at one liveweight level. These factors are considered further in the present study.

Fletcher (1974) found that the mean ovulation rate of a flock of Koonoona ewes in summer was influenced by the nutritional conditions that they experienced during the preceding winter. Three similar groups of ewes were grazed at either high, moderate or low levels of nutrition between March and the end of September. At the end of this period medium ewes were 4.8 kg lighter than high ewes while low ewes were a further 10.8 kg lighter than medium ewes. All groups returned to a similar mean liveweight level by the end of December and ovulation was recorded a month later. Ovulation among the ewes previously on low nutrition (1.28) was lower than for the previously medium (1.57) or high (1.61) ewes.

This finding casts doubt on the validity of applying the results of short term experiments relating ovulation and liveweight to a grazing situation where mean liveweight at ovulation can be preceded by one of numerous different nutritional pathways.

Previous measurements of nutritional conditions, or animal status, may be helpful in adjusting a prediction of ovulation based solely on liveweight. However, such measurements are unlikely to be suitable for commercial use because of the spread in time over which they would be required. It would be preferable to be able to measure other factors in the animal at the same time as liveweight and use them in conjunction with liveweight to predict ovulatory performance at that time. The usefulness of the body components of water, lean, protein and fat as additional factors is considered in the present study.

Fletcher (1971) found that the ovulation rate of Koonoona ewes was related not only to liveweight at ovulation but also to 'inherent liveweight'. Inherently heavier ewes had more twin ovulations, with an average increase of about 1.3 per cent for each 1 kg increase in liveweight. The experimental design did not allow him to partition the response between differences in (inherent) body size and body condition at ovulation. Thus data were generated in the present study to allow some consideration of within-flock relationships between ovulation rate and liveweight, body size and body condition.

BODY COMPOSITION

C. BODY COMPOSITION OF LIVE SHEEP

1. ESTIMATION OF BODY COMPOSITION IN LIVE SHEEP

The estimation of body composition of live sheep, in terms of the body components of fat, protein, lean and water, can be made using a simple procedure that requires little interference with the animals concerned. The method requires the measurement of two parameters after a period of fasting, namely, total body water (TBW) and liveweight. These parameters can then be used in mathematical equations to predict the weight of body components (TBW, fat, protein, lean, ash) and the energy value (Panaretto, 1963, 1968; Panaretto and Till, 1963; Keenan, McManus and Freer, 1969; Reardon, 1969; Searle, 1970a, 1970b) of the animals.

(a) Total body water and its measurement

Total body water (TBW) is the volume of water found in the gut, cells and extracellular spaces of an animal. The volume of TBW is not constant but is in a continuing state of adjustment as the animal balances its water intake and water loss. An animal may gain water by drinking, by eating food containing water, by utilizing metabolic water formed during the combustion of food and by small amounts that may enter through the respiratory tract and skin. It may lose water through urine, faeces, milk and from the skin, either by diffusion, by secretion of sweat or by evaporation to air expelled from the respiratory tract.

The TBW of an animal can be measured after death by drying. This, the oldest method of determining TBW, is obviously unsuitable for making measurements on a live animal. To overcome this problem a number of substances have been investigated for use in what is often called the dilution technique. This technique relies on an injected substance becoming evenly distributed throughout the TBW and then using the general formula

$$\text{Volume TBW} = \frac{\text{Amount of test substance injected}}{\text{Concentration per unit volume of test substance after even distribution (equilibration)}}$$

to determine the volume of TBW.

Inaccuracy in the estimate of TBW using this technique can arise if the substance injected is not completely confined to the TBW, is excluded from some sections of TBW, is metabolised or is excreted.

Substances that have been used to measure TBW include urea, thiourea, antipyrine, N-acetyl-4-amino-antipyrine, and the isotopes of hydrogen as deuterium or tritium oxide. Urea and theiourea provide the least accurate and reliable estimates.

Panaretto and Till (1963) compared the accuracy of *in vivo* estimates of TBW in goats made using antipyrine (AP), N-acetyl-4-amino-antipyrine (NAAP) and tritiated water (TOH) with TBW determined by desiccation. They found that TOH provided an accurate and unbiased estimate of TBW while both AP and NAAP spaces provided biased estimates.

Deuterium oxide and TOH have a similar distribution volume and equilibration occurs at the same rate, so from the point of view of accuracy they are equally suitable tracer substances (Hansard, 1964). However, the technique for preparing TOH samples for counting is less elaborate than for deuterium oxide and with the development of liquid scintillation counters TOH is now the preferred substance.

The equilibration time for TOH, in mature sheep, has been shown variously to be 5 hours (Till and Downes, 1962) and 5 to 6 hours (Macfarlane, Dolling and Howard, 1966) after an intravenous injection. In new-born lambs equilibration has been found to occur in 2 hours (Searle, 1970a).

There are small losses of tritium oxide from the animal during the equilibration time due to evaporation, to excretion of urine and faeces, and to incorporation in tissue. All these losses are small, in sheep totalling overall only 2 to 3 per cent (Till and Downes, 1962). Such losses result in a 'TOH space' value that over-estimates the true value for TBW. A simple correction can be applied in calculating the estimate of TBW.

(b) Relationships between TBW, fasted liveweight and body components

Several methods, using the measurement of TBW (or the uncorrected 'TOH space' value) and liveweight in the fasted animal, have been used to predict the weight of body components.

For example, Panaretto (1968) used the TBW value in a relationship between TBW (as a percentage of liveweight) and fat (as a percentage of liveweight) to estimate the weight of fat in the animal. He then obtained an estimate of fat-free dry matter by difference and corrected it by 1.5 per cent of bodyweight to account for dry solids in the gut. The protein content of this corrected value for fat-free dry matter was found to be 77 per cent. Ash was determined by difference. This is an "indirect" method in that the fat component is not estimated directly from the two measurements made on the animal. In contrast, Searle (1970a) derived multiple regression equations that estimate the components directly from values of 'TOH space' and fasted liveweight.

(c) Assumptions and reliability of prediction equations

All methods of estimating body components from these measurements assume several basic relationships, namely, that TBW comprises a constant proportion of the fat-free empty body and is unaffected by the fatness of the animal, that there is a constant proportion of protein in the fat-free dry body and that the dry matter content of the gut can be regarded as constant. Measures of these factors reported in the literature include: for percentage water in the fat-free empty body, 72.8 per cent (range for individuals 70.9 - 74.7%) (Hight and Barton, 1965), 71.7 per cent (range for groups 71.3 - 72.3%) (Keenan *et al.*, 1969) and 73.8 per cent (Searle, 1970a); for percentage protein in the fat-free dry matter, 76.9 per cent (Panaretta, 1968), 76.6 per cent (Panaretto, 1963), 75.3 per cent (range for groups 73.6 - 76.6%) (Keenan *et al.*, 1969) and for dry matter content of the gut (as a percentage of body weight), 1.2 per cent for ewes and 1.5 per cent for wethers (Panaretto, 1968) and 0.7 per cent in ewes (Panaretto, 1963).

The proportions of both water in the fat-free empty body and protein in the fat-free dry matter is affected by the age of the animal up to about 9 months of age, but from then on there is no further effect (Searle, 1970a).

Searle (1970a) derived prediction equations for young sheep up to the age of 18 months and found that they were comparable with those derived from adult animals studied by Panaretto (1968). He then combined the two sets of data and derived broadly based equations, using fasted

TOH space and liveweight, that he concluded offered "the most reliable means of predicting the body composition of sheep irrespective of age".

Searle did note, however, that the inclusion of an age parameter increased the correlation coefficient for each component. Except in the case of ash, he considered the improvement too small to warrant the inclusion of an additional parameter. Donnally and Freer (1974) have also investigated the use of an age parameter. They defined what they called a maturity factor, as the age of the sheep as a proportion of the age at which mature size is reached. They examined their own data together with previously published data (from Keenan (1967), Panaretto (1968), Searle (1970a, 1970b) and Farrell and Reardon (1972)) and concluded that the inclusion of maturity substantially reduced the residual standard deviation compared with regression models that include only fasted liveweight and tritiated water space.

Work by Farrell and Reardon (1972) suggests that the predicted values for the various body components may also be unreliable (inaccurate) in severely undernourished adult sheep. They examined the body components of well-fed (27% chemical fat) and grossly undernourished (9% and 5% chemical fat) Merino ewes in detail and found that there was a significantly greater percentage of water in the fat-free empty body of the undernourished ewes. This, of course, negates one of the basic assumptions of the prediction method, and when it occurs will cause an overestimation of protein and underestimation of fat. Farrell and Reardon therefore suggest that separate equations should be used for undernourished animals although it seems that this may be necessary only in instances where animals are in very poor condition. Hight and Barton (1965), for example, were unable to detect differences in the mean water content of the fat-free bodies of Romney sheep where undernutrition reduced the amount of fat from 32 to 24 per cent.

It should be noted that if separate equations are used for undernourished animals then there will be discontinuities in predicted values for sheep experiencing large changes in their state of nutrition. This circumstance would be avoided if a 'condition' factor could be included in the general prediction equations.

2. NUTRITION AND SEASON EFFECTS ON BODY COMPOSITION

Several studies have shown that severe changes in the thermal or nutritional environment can affect the composition of sheep over a short period, but the effect of less severe loss and regain of liveweight, on a seasonal basis, has received scant attention, especially in mature animals. Morris, Howard and Macfarlane (1962) found that Peppin Merino wethers shorn during winter responded in different ways depending on their nutritional status. While those in a poorer state (higher stocking rate) lost three times as much solids (5.8 kg) as others in a fatter condition (lower stocking rate) (1.75 kg) the loss was hardly apparent on a liveweight basis (difference of only 0.6 kg) as a result of an accumulation of water among the poorer wethers. Shearing during summer has been shown to cause a readjustment of the distribution of water within the body but not to affect the total amount of body water (Macfarlane, Howard and Morris, 1966).

Keenan, McManus and Freer (1969) studied 3-year-old Peppin wethers that lost 16 per cent of their liveweight over four weeks, maintained the loss for eight weeks and then regained it over the following five weeks. The liveweight lost consisted of 45 per cent water, 39 per cent fat and

13 per cent protein but that regained consisted of 60 per cent water, 23 per cent fat and 12 per cent protein: only 75 per cent of the energy lost was regained. Hight and Barton (1965) studied the effects of undernutrition and realimentation in Romney ewes and found that there was a non-significant reduction in the weight and percentage of carcase fat. Carcase protein was reduced by both 21 days and 42 days of undernutrition, although the reduction was not significantly greater after 42 days than after 21 days. Realimentation increased the weight of carcase protein but the amount was still significantly lower than in the control group. The weight, but not proportion, of carcase water was reduced by the first 21 days of undernutrition but was not further reduced by continuing undernutrition. Realimentation increased the weight of water to about that of the control animals. These reports contrast with that by Meyer and Clawson (1964) who found that 5-month-old wethers had a striking loss of protein when placed on a restricted diet for six weeks. When compared at a similar liveweight the fasted and realimented animals had a larger quantity, and proportion, of body fat (and energy) compared with the continuously grown control animals.

The situation for young sheep undergoing severe nutritional changes has become clearer since the present study was undertaken. Drew and Reid (1975) studied wether lambs underfed for a period of ten weeks to lose about 25 per cent of their initial liveweight. They found that the initial losses were of water and protein and that lipolysis was substantial only during the second half of the undernutrition period. Regrowth over the first 15 days of realimentation was almost entirely attributable to increases in water and protein. After this time the fat component increased at a rate similar to that expected in a continuously growing animal of similar liveweight. The initial response in water and protein persisted until the starved animals reached the liveweight of the controls: they then had more protein and less fat. Drew and Reid noted that there was no fat loss until at least 12-15 per cent of the empty body weight had been lost, and suggested that a decreased fat content after realimentation would be unlikely unless there was a weight loss of at least this magnitude.

Black (1974), using computer modelling studies, has shown that many of the conflicting reports of nutritional effects on body composition can be explained with an understanding of the interrelationships between nutrient intake, stage of animal maturity, and the partition of energy between the needs for maintenance and both protein and fat synthesis. Black's studies suggest that sheep losing weight rapidly or slowly will contain, respectively, more or less fat than similar weight animals not subjected to the weight loss. This conclusion in relation to young animals is consistent with the findings, in mature wethers, of Keenan, McManus and Freer (1969) as mentioned above, and with that of Searle, Graham and O'Callaghan (1972) who reconsidered the data of Panaretto (1964) and Graham (1967).

There is no evidence that there is a direct effect of season on these nutritional effects. However, fluctuating nutritional conditions would, as a secondary effect of season, cause seasonal variation in the composition of the ewes. In addition to these uncertain effects there is a specific effect of season on the amount of total body water, with the volume being greater in summer than winter (Macfarlane and Howard, 1970).

3. BODY COMPOSITION IN THE PRESENT STUDY

In view of the likely effects of nutrition and season on body composition, and in turn possibly on ovulatory performance, the composition of a number of ewes in the present study was measured using the prediction equations, based on tritiated water space and fasted liveweight, derived by Searle (1970a). The data generated were examined for seasonal variation in the components of each treatment group and for relationships between individual components and the concurrently observed ovulatory performance.

EXPERIMENTAL

III. EXPERIMENTAL

1. BASIC DESIGN

The basic experimental design comprised four treatment groups, each of about 65 ewes. Three of the groups were fed a hay/grain ration while being confined in small yards (Pen groups) and the fourth was set stocked in a field under normal commercial conditions (Field group).

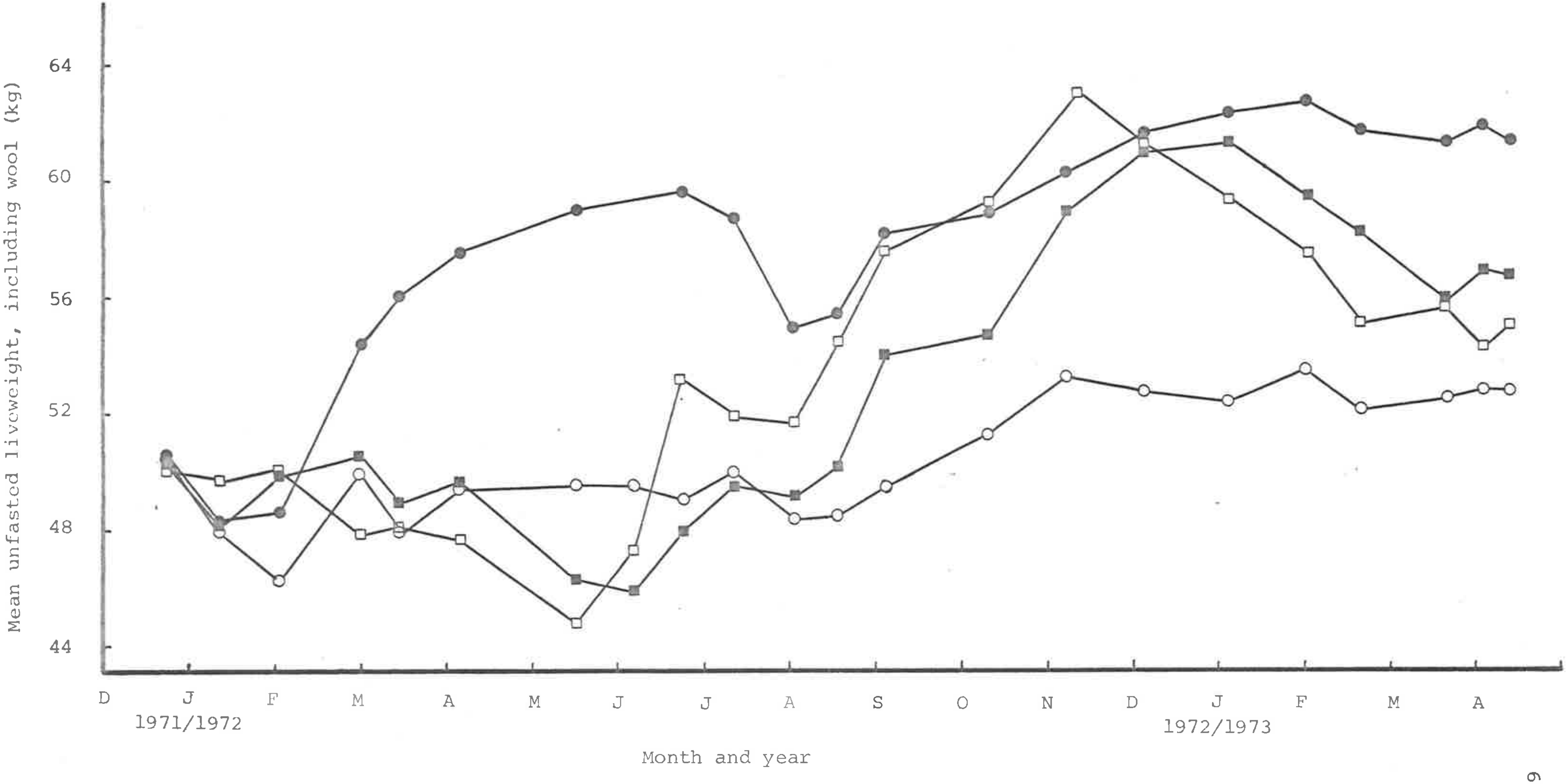
Theoretically, the mean liveweight of two of the pen groups was maintained at one of two constant levels throughout the experiment (High and Low groups) while that of the remaining group was adjusted to closely follow the seasonal pattern of mean liveweight experienced by the Field group (Variable group). The two levels of constant liveweight chosen were those expected to be the minimum and maximum mean liveweight levels attained by the Field group in a year of normal seasonal conditions. The mean liveweight recorded for each of the four groups throughout the experimental period, from December 1971 until April 1973, are tabulated in Appendix Table 1 and illustrated in Figure 1.

2. AIMS

The aims of the study can be summarised as follows:-

(i) to determine the level of oestrous and ovulatory activity, at the expected seasons of maximum and minimum sexual activity, in four groups of ewes: one group being grazed in the field (Field group) and three being maintained in small yards; one group of which fluctuated in liveweight in a manner similar to the Field group (Variable group)

Figure 1. The mean unfasted liveweight (kg), including wool, of surviving ewes in the Low (○), High (●), Variable (■) and Field (□) groups. Only weights recorded at about three weekly intervals are depicted. All weights recorded are tabulated in Appendix Table 1.


Mean unfasted liveweight, including wool (kg)
64
60
56
52
48
44
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
1971/1972
1972/1973
Month and year

and two that were maintained at one of two liveweights throughout the year (High and Low groups).

(ii) to compare the oestrous and ovulatory performance of (a) the two constant liveweight groups (High and Low) with the performance of similar ewes in a previous year, (b) the two constant liveweight groups with the penned group allowed to fluctuate in liveweight (Variable), and (c) the two groups with fluctuating liveweight (Variable and Field).

(iii) to investigate whether the levels of ovulatory activity determined in (i) above were related to the mean liveweight and, or, the mean body condition index at ovulation.

(iv) to determine whether there were seasonal changes in the mean amounts of the body components of water, lean, protein and fat and to consider whether the changes observed in one or more of the components provides a basis for improving the relationships assessed in (iii) above.

(v) to investigate, on a within-flock (within-treatment) basis, whether the mean level of ovulatory activity was related to the mean level of either liveweight or body condition index at ovulation, or to body size.

(vi) to investigate, among the Variable and Field ewes, whether there was a relationship between the level of multiple ovulation and the rate of water turnover in either March or October.

3. MATERIALS AND METHODS

(a) Location and environmental conditions

The experiment was conducted at the Turretfield Research Centre of the South Australian Department of Agriculture at Rosedale (34° 33'S 138° 50'E) between November 1971 and March 1973. Turretfield is located about 50 km NNE of Adelaide on the southern edge of the cereal/animal mixed farming zone of the Mid-Northern area of South Australia. It has an average annual rainfall of 459 mm (average for 70 years) with a marked winter incidence of rainfall and summer-autumn drought, typical of the Mediterranean environment. Long term average monthly rainfall, together with maximum and minimum temperatures, are shown in Appendix Table 1, while data covering the specific period of the experiment are shown in Appendix Tables 3 and 4.

(b) Animals

Two hundred and sixty six South Australian Strong-wool Merino ewes were used in the experiment. They were drawn from a flock founded at Turretfield in 1958 on ewes bought from the "Koonoona" stud and subsequently joined each year to "Koonoona" flock rams. Ninety nine of the ewes were born in June 1967 (1967 ewes) and the remaining 167 in June 1968 (1968 ewes). The 1968 ewes had been running as two distinct flocks prior to their involvement in this experiment and were treated, for the purposes of randomisation, as two separate flocks of 99 (1968 A ewes), and 68 ewes (1968 B ewes).

(c) Randomisation

The ewes were randomised, within each of the three groups 1967 ewes, 1968 A ewes and 1968 B ewes, into four treatment groups on the basis of their fasted liveweight measured pre-shearing and their body size (see (g) below) measured post-shearing in December 1971 (1967 ewes weighed 24/11/71, 1968 A ewes weighed 30/11/71, 1968 B ewes weighed 8/12/71: all ewes measured 16 and 17/12/71).

The body weight and body size data were plotted on a large sheet of graph paper together with the identity of the ewe associated with each set of data. A linear regression line of body weight on body size was calculated and drawn on the graph. Two straight lines were then drawn by hand, parallel to, and equi-distant on either side of, the regression line such that about 90% of the points were included within the lines. Lines were then drawn between those two lines, perpendicular to the regression line, to form groups of four ewes (perpendicular quadruples). Further groups of four (parallel quadruples) were formed on either side of the perpendicular quadruples by drawing additional lines parallel to the regression line but further from it than the previously drawn lines. Ewes in each perpendicular and parallel quadruple were allocated at random within quadruple to one of the four treatment groups.

Eighty four ewes included in 21 perpendicular quadruples were selected for the study of body composition: 12 quadruples were selected from the 1968 A ewes and 9 from the 1968 B ewes. Within each group of ewes one third of the quadruples were selected as a block of the heaviest/largest ewes, one third as a block of the lightest/smallest ewes and the remaining third as a block of middle weight/middle size ewes. There were thus 21 ewes in each treatment group (selected ewes).

(d) Treatment groups

There were four groups of ewes, each initially comprising about 65 ewes and each subjected to one of the following treatments, over a 16 month period from 23 December 1971 until 12 April 1973. One group grazed in the field while the other three were confined in small yards and fed on a hay/grain ration.

Treatment 1. The ewes were hand fed a hay/grain ration, on a group basis, in a small yard with the aim of attaining, and then maintaining, a constant group average wool-free liveweight throughout the experiment of about 55 kg (referred to as High).

Treatment 2. As for treatment 1, but to maintain a liveweight of about 45 kg (referred to as Low).

Treatment 3. As for treatment 1, but with the aim of varying the quantity of feed available so that the group average wool-free liveweight followed a similar seasonal pattern to that of the Field ewes (see treatment 4 below) (referred to as Variable).

Treatment 4. The ewes were set stocked in a paddock (10.3 ha) of subterranean clover pasture trashseeded in autumn 1971 after two successive crops of barley (*Trifolium subterranean* cv. Clare 4.5 kg/ha, cv. Woogenellup 2.2 kg/ha, cv. Geraldton 3.4 kg/ha). Superphosphate fertilizer (7.6% water soluble P, 1.0% citrate soluble P, 11.0% total S) was applied at the rate of 100 kg/ha both at the time of seeding in 1971 and in autumn 1972. The paddock had been treated with about 3 600 kg/ha of superphosphate since fertilizer was first applied in 1923; the last 1 600 kg/ha was applied since 1956 (referred to as Field).

Ewes allocated to treatments 1, 2 and 3 were held in three small yards, each of about 0.1 ha in area, located together on gently sloping alluvial sandy soil with an open southerly aspect. A portion (approx. 20%)

of each of the yards containing groups 1 and 2 was subjected to severe waterlogging following rain during the winter of 1972 which made conditions uncomfortable for those ewes.

(e) Feeding of penned ewes

In an effort to ensure that all ewes would consume a similar diet and not be able to selectively eat either grain or hay it was planned that they should be fed a ration comprising 1 part of pasture hay, 1 part of barley grain and 1 part of oaten grain prepared by hammer-milling each component in turn through a 25 mm screen before being mixed together in a feed mixer. After feeding this ration for about six weeks it became obvious that the sheep were not thriving: even those on unrestricted feeding, on average, lost weight and several animals died.

In an attempt to overcome this situation changes were made to the diet. Firstly a ration was prepared in which only the hay was hammer-milled and then mixed with whole grain. After this ration was offered for two weeks, further deaths occurred and so baled hay was offered in racks as well as the ration in the feed troughs. It was immediately obvious that the ewes preferred the hay to the hammer-milled hay plus grain mixture. Thus hay, together with varying amount of the hay/grain mix, was fed *ad libitum* to all three groups for about a week. Despite the fact that several more sheep died during that week it appeared that the flocks in general were thriving on this ration. Thus it was decided to feed a ration comprising about 25 per cent pasture hay (fed in open racks) and 10 per cent hammer-milled hay and 65 per cent whole grain (½ barley and ½ oats) by weight (fed in sheltered troughs). This ration proved to be acceptable to the animals and was used for the remainder of the experiment. All rations were supplemented with common salt (approx. 0.2%) and finely ground limestone (approx. 1.5%). All ewes were injected intramuscularly with 125,000 i.u. of Vitamin A (E.R. Squibb and Sons, Pty Ltd) in both June 1972 and January 1973.

Each of the three groups of ewes were fed three times a week, with 1.5 times the amount of feed being offered on Friday as on Monday and Wednesday. The amount of feed was measured out on the basis of "level 5-gallon bucketfulls" of hay/grain mix, and bales of hay, each of known average weight. The rate of feeding was reviewed each time the ewes were weighed, and increased or decreased slightly to achieve the desired changes in group mean liveweight.

(f) Liveweight measurements

As the design of the experiment depended on the group mean liveweights follow predetermined patterns, the ewes in all groups were weighed frequently to determine departures from these patterns: ewes were often weighed weekly but sometimes fortnightly. Departures from the desired liveweight were corrected by adjusting the amount of feed offered to the groups. All of the mean liveweights recorded for each of the four groups over the course of the experiment are tabulated in Appendix Table 1 while a proportion of them are shown in Figure 1 (observations less than three weeks apart have usually been omitted).

The ewes were weighed on Tuesday mornings providing that the weather was fine and they were dry. If they were wet the weighing was postponed until Thursday. These two days were chosen because the ewes would have a reasonable gut fill and all groups would be directly comparable. Fasted liveweight would have provided a better basis for between group comparisons. This was not routinely taken because it would have involved fasting the Field, and on some occasions the High and Variable groups and, because of the frequency of weighing (fasting), would have altered the treatments considerably.

However, 22-hour fasted liveweights were measured, for all ewes at each of the nine times that body composition and water turnover estimates were made (see later sections). On each of these occasions all ewes were removed from both feed and water from late on Monday afternoon until Wednesday morning: a period of about 40 hours.

Two types of corrections to the recorded liveweights were used in assessing the results of this experiment. Firstly, corrections were derived to account for the difference between the normal Tuesday or Thursday weight and the fasted liveweight taken on Tuesday afternoon. Secondly, estimates of average greasy wool weight were made from measurements of wool growth taken at several times during the experiment, using dye banding studies, and total greasy fleece weight grown over the duration of the experiment. Steady rates of wool growth were assumed between successive dye bands. The corrections applied are shown in Appendix Table 5.

Estimates of wool-free fasted liveweight, and hence body condition index, at ovulation were calculated by applying the above corrections to individual measurements of liveweight made up to 14 days prior to ovulation.

(g) Body size measurements

The length, breadth and depth of each ewe was measured at both the beginning and end of the experiment using a pair of large calipers. On both occasions the ewes had been shorn a few days previously. These sets of measurements were then used to calculate body size using the following formula (Turner *et al.*, 1953):

$$\text{body size} = \text{length} \times \text{depth} \times \left(\frac{(\text{width at hips}) + (\text{width at shoulders})}{2}\right)$$

where the various measurements are defined as:

(i) length - the distance from the most anterior palpable spinous process of the thoracic vertebrae, commonly found in front of, and between, the scapulae, to either sciatic tuber.

(ii) depth - the vertical distance from the highest point of the wither to the ventral surface of the sternum.

(iii) width at hips - the distance from the point of the ilium which is furthest from the midline of the back (i.e. the tuber coxae) on one side to the corresponding point on the other side.

(iv) width at shoulders - the maximum distance between the lateral tuberosity of one humerus to the corresponding point on the other.

(h) Oestrus

The incidence and pattern of occurrence of oestrus was determined at each of the three times using vasectomised rams, each fitted with a Sire Sine harness and crayon (Radford, Watson and Wood, 1960). The rams were joined on 23 February, 1972, for five weeks; on 23 August, 1972, for six weeks, and on 16 February, 1973, for five weeks. Two rams were placed with each group of ewes and rotated between groups each time the occurrence of oestrus was recorded. Sire Sine crayons were changed to a different colour fortnightly. The identity of each ewe having a fresh unrecorded crayon mark on the rump (detected in oestrus) was recorded each Monday, Wednesday and Friday.

The eight vasectomised rams used in each set of observations of oestrus were selected at random from a flock of about 20 and were not the same set of rams on each occasion. Rams, either vasectomised or entire, were not allowed near any of the four groups of ewes at any time during the experiment other than when observations of oestrus were being made.

(i) Ovulation

The ovaries of all ewes were examined by laparoscopy on each of the three occasions at which oestrus was recorded. The number, and date, of each set of observations is shown in Table 1.

The examination was conducted between three and seven days after the second recorded oestrus or, in the case of ewes with no recorded oestrus, at the end of the oestrus recording period. At each examination the number of *corpora lutea* were recorded. Each *corpus luteum* was assumed to indicate the release of one ovum.

Ewes were removed from feed the afternoon before the examination to ensure that each ewe had a relatively empty rumen. (This makes observation easier.) Immediately prior to examination the belly wool was removed with commercial shearing machinery and the ewe was restrained in a laparotomy cradle (Lamond and Urquhart, 1961). The cradle was modified so that the hind legs could be held about 15 cm higher than that shown in the diagram of Lamond and Urquhart. A small area anterior to the udder and on both sides of the mid-line was swabbed with Savlon antiseptic (Hospital concentrate - ICI Australia Ltd) and clipped with small animal clippers. A local anaesthetic, xylocaine 2 per cent with adrenaline (Astra Pharmaceuticals Australia Pty Ltd), was injected around the sites where the two cannulae were to be inserted. The larger cannula (9 mm diameter) was inserted just to the left of the mid-line and anterior to the udder while the smaller one (5 mm diameter) was inserted about 5 cm on the right side of the mid-line and level with the anterior edge of the udder. A 7.5 mm diameter, 30 cm long, 30° oblique vision telescope attached by a fibre optic cable to a matching light source (Genito-urinary Manf. Co. Ltd, England) was inserted down the larger cannula. A pair of grasping forceps (35 cm long), used for manipulating the reproductive tract, was inserted through the smaller cannula. The larger cannula was fitted with a stop-cock and valve through which air was introduced into the abdominal cavity using a hand operated bellows. This forced the rumen and fat anteriorly so that the reproductive tract could be seen more easily. Following the examination the two wounds were dusted with Cicatrin antibiotic powder (Calmic Aust. Pty Ltd) and the larger one was closed using a single Michel clip. Each ewe was returned to her respective treatment area later in the day.

(j) Body condition index

An index of body condition was calculated for individual ewes as follows:

$$\text{Body condition index} = \frac{\text{Wool-free, fasted liveweight (g)}}{\text{Body size (cubic cm)}}$$

where body size (as defined in (g) above)

$$= \text{length (cm)} \times \text{depth (cm)} \times \frac{\text{(width at hips + width at shoulders)}}{2}$$

(k) Body composition and water turnover

The body composition (lean, protein, water, fat) and water turnover of each survivor of the 84 ewes originally selected for the body composition studies (Selected ewes) (see Section (c) above) was estimated at nine times during the experiment. Estimates were also made for each of the remaining ewes in both the Field and Variable groups at two of the nine times, namely, those immediately following the two sets of observations on oestrus and ovulation made during spring 1972 and autumn 1973. The number of observations, together with the dates at which they were made, are shown in Table 1.

Estimates of the body components of water, fat, protein and lean were made for each ewe by determining the TOH space and wool-free, fasted, liveweight and then applying these values in the equations derived by Searle (1970a). Namely,

$$\text{Total body water (TBW)} = 0.92x - 0.01$$

$$\text{Fat} = 1.14x + 0.95y + 0.16$$

$$\text{Protein} = 0.117x + 0.056y + 0.154$$

$$\text{Lean} = 1.24x - 0.46$$

where x = TOH space (kg)

and y = Wool-free, fasted, liveweight.

Water turnover was calculated from the same measurements as used for estimating body composition, together with a further measurement of TOH concentration made seven days after the initial measurement.

Estimates of body composition and water turnover were made as follows. Penned animals were allowed normal access to their Monday ration from the time they were fed at about 0900 h until late on Monday afternoon (approx. 1600 h). At that time all ewes, including those in the Field treatment, were yarded so that they no longer had access to either feed or water. On Tuesday afternoon the relevant ewes in each group were injected intramuscularly with 2 ml of TOH (activity approx. 100 µ C/ml) and all the ewes were weighed (approx. 22-hour fasted liveweight). The

Table 1. The date and number of measurements taken of body composition and water turnover, and of ovulation, for each treatment group at each time of measurement.

Date of measurement	Treatment group Low Selected[a]	 Low Other	 High Selected	 High Other	 Variable Selected	 Variable Other	 Field Selected	 Field Other
(a) Body composition and water turnover (No. ewes measured)								
12 and 19.1.72 (Time 0)	21	-	21	-	21	-	21	-
5 and 12.4.72 (Time 1)	20	-	21	-	20	-	21	-
17 and 24.5.72 (Time 2)	19	-	21	-	20	-	21	-
12 and 19.7.72 (Time 3)	20	-	20	-	18	-	19	-
6 and 12.9.72 (Time 4)	19	-	19	-	18	-	19	-
11 and 18.10.72 (Time 5)	18	-	19	-	18	35	19	38
6 and 13.12.72 (Time 6)	19	-	18	-	18	-	18	-
21 and 28.2.73 (Time 7)	19	-	18	-	18	-	18	-
4 and 11.4.73 (Time 8)	19	-	18	-	16	34	19	38
(b) Ovulation (No. ewes examined)[b]								
15 to 30.3.72	19	39	21	38	20	39	21	44
13.9 to 5.10.72	20	36	19	37	18	36	19	39
7 to 27.3.73	20	35	18	35	17	36	19	37

[a] Ewes selected for detailed study of seasonal changes in body composition.

[b] Excludes several ewes examined but in which the ovaries could not be observed because of excessive fat or adhesions.

dose of TOH was allowed to equilibrate overnight. On Wednesday morning, before the ewes were allowed access to either feed or water, a 10 ml blood sample was taken from the jugular vein of each ewe injected (referred to being sampled at time T_0). Each sample was collected in a heparinised 10 ml plastic centrifuge tube and shaken gently to prevent clotting. Blood was sampled from groups of ewes in the same order as they were injected so that the equilibration time was similar for each group (about 19 h). A further 10 ml blood sample was taken immediately before the penned animals were fed on the following Wednesday (referred to as being sampled at time T_7).

The plasma in each blood sample was separated by centrifugation and drawn off using a Pasteur pipette into a 5 ml plastic tube within 4 hours of collection. Unless plasma samples were scheduled for measurement of radioactivity within several days they were stored at minus 16°C, and thawed during the night before processing.

At processing an aliquot (0.5 ml) of each plasma sample was accurately dispensed by means of a graduated 1 ml pipette into a 10 ml plastic centrifuge tube containing 8 ml of scintillation fluid. The scintillation fluid, prepared by mixing together 250 ml ethanol, 375 ml dioxane, 375 ml toluene, 80 g naphthalene and 5 g of 2,5-diphenyl oxazole (PPO), causes the solids in the plasma to precipitate. Each tube was capped and gently shaken to ensure complete mixing and then centrifuged, at approximately 1,100 g for 10 minutes at 4°C, to consolidate the precipitate. The remaining liquid was decanted into a glass scintillation vial and the activity of each sample was measured by counting for 10 minutes in a Hewlett Packard Tri-Carb Scintillation Spectrometer Model 3002.

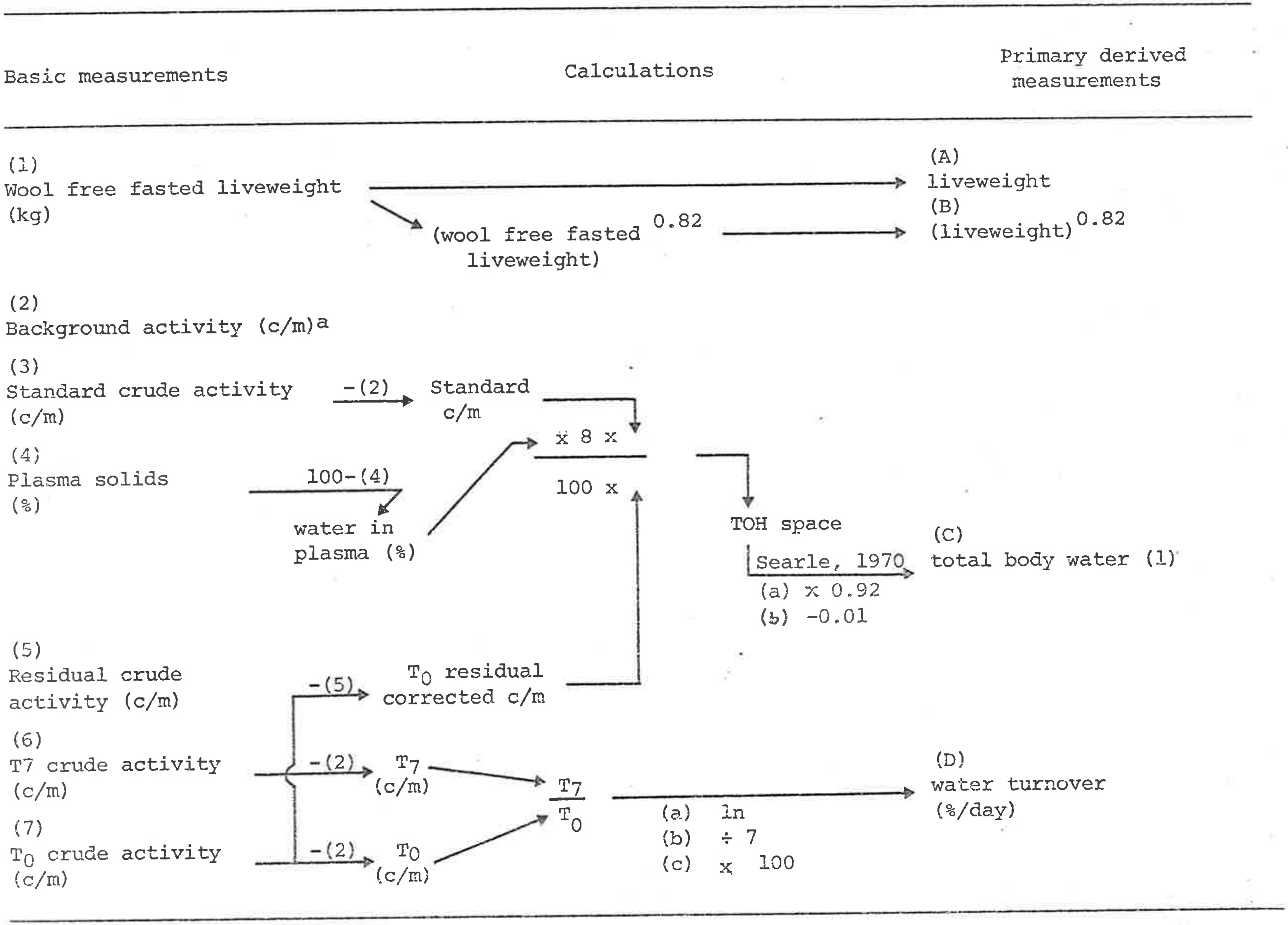
Whenever there was a possibility of residual activity from previous doses of TOH, blood samples were taken from eight randomly selected ewes in each treatment group immediately before they were further treated with TOH. The average activity of these samples was used to correct the T_0 activity for all ewes of the relevant treatment group (residual blank). Two vials prepared using 0.5 ml of distilled water instead of plasma were included in each run of samples to determine an average background level of activity for each run (background blank). This activity was used to correct the activity of T_0, T_7 and standard samples.

A standard solution of TOH was prepared with an activity 1/4000 of that injected into the ewes (approx. 25 mu C/ml) and duplicate samples were included in each run counted.

The volume of water mixed with the scintillation fluid, and of which the activity was counted, was less than 0.5 ml because of the presence of solids in the plasma. Thus a correction was estimated for each treatment group at each of the nine times of sampling. Duplicate 2 ml samples of plasma from several ewes (usually eight) were dried in open Petri dishes at 44°C overnight and the weight of solids was determined immediately upon removal from the oven. Corrections for plasma solids ranging from 8.3 per cent to 9.9 per cent were found necessary. The values are tabulated in Appendix Table 6.

The methods used to calculate the primary measurements required for calculating body composition and water turnover data, from the measurements described in this section, are shown diagramatically in Figure 2.

Figure 2: Diagrammatical representation of calculations used in deriving the primary measurements required for calculating body composition and water turnover data.



a counts/minute.

(1) Statistical analysis

The details of the analyses used for each section of the study (oestrus, ovulation, body composition, within-flock comparisons) are provided in the appropriate section of the Results and Discussion chapter.

In general, between-treatment effects on the occurrence of oestrus, the incidence of anovular ewes and the incidence of multiple ovulating ewes were examined using chi-square analyses. Seasonal changes in body composition and water turnover, and within-flock relationships between ovulation and water turnover, body size, body condition and liveweight were examined using analysis of variance and regression techniques.

It should be noted that the same ewes were observed repeatedly. While this was a deliberate, and essential, plan to provide sufficient numbers of ewes in each treatment to obtain useful estimates of biological parameters - in particular ovulation rate and the incidence of oestrus - it complicates interpretation of some statistical analyses. The significance of within-treatment differences between times of observation may be greater than that indicated by the analysis, as the between group variation is likely to be less than expected between independent groups, i.e. less than that for which the analysis is designed. Comparisons between-treatments at any one time of observation are between independent groups and are subject to the forms of variation expected in the analysis.

The repeated occurrence of a between-treatment difference, at different times of observation, must not be considered as a repeated experiment, nor interpreted as evidence for the effect having been detected among a wider cross-section of Koonoona ewes. It (repeated occurrence) should not be misconstrued as a replication, either. There is no replication. A between-treatment effect could occur at successive observations simply as a result of accidental bias in the initial allocation of ewes to treatment groups.

RESULTS AND DISCUSSION

OESTRUS

IV. RESULTS AND DISCUSSION

A. OESTRUS

Statistical analyses were performed on data relating to 222 ewes present at all three sets of observations (March, 1972, September, 1972, March, 1973). Observations made on 26 ewes in March 1972 (Low, 3; High, 6; Variable, 8; Field, 9) and on 3 in September 1972 (High, 3) were excluded from the analysis as they died before the final set of observations were taken.

The incidence of oestrus was examined using chi-square analyses. In all single degree of freedom comparisons involving an expected value of less than 10 an additional value of chi-square was calculated using Yates' Correction for Continuity (χ_c^2). Corrected values have been shown only where their use alters the significance of the comparison.

The pattern of occurrence of oestrus among each group at each time was examined by reference to the shape of the accumulated incidence of detected oestrus (as graphed in Figures 3 to 9) and by chi-square analysis of the incidence to both day 16 and day 35 after the introduction of rams. Examination of the incidence to day 16 was chosen as the ewes detected during this period would not have exhibited oestrus as a result of ram stimulation. If the incidence had been determined at day 17, or later, some ewes could have been stimulated by the sudden association with rams. The observed incidence was therefore indicative of the level of oestrus activity that would have occurred, but passed undetected, if rams had not been joined. A similar level of activity would have been expected if the ewes had been associated with rams for a prolonged period.

1. RESULTS

(a) Effect of treatment (within time of joining)

The accumulated incidence of oestrus, among all four treatment groups, is depicted individually for each time of joining in Figures 3, 4 and 5, and presented numerically in Appendix Tables 7a, 7b and 7c.

It appears from Figures 3 and 5 that there was a similar pattern of occurrence of oestrus in each of the four groups during both March 1972 and March 1973. At both times a high proportion (70 to 90%) of the ewes in each group were detected by day 35. In September 1972 the pattern of oestrus varied between treatment groups (Figure 4). The Field group, and to a lesser extent the Low group, each showed a marked synchronisation of oestrus following day 16. The High and Variable groups did not.

Data relating specifically to the incidence of oestrus to either day 16, or day 35, of joining are shown in Table 2. The incidence to day 16 was similar among each treatment in either March 1972 or March 1973, but in September 1972 the groups were not homogeneous ($\chi^2_3 = 19.31$; $P < 0.001$). In September the three pen-fed groups were homogeneous and the pooled incidence for these three groups (50.0%) were significantly higher than for the Field group (20.7%) ($P < 0.001$).

The incidence of oestrus to day 35 was similar among all groups at each time of joining.

Figure 3. The accumulated percentage incidence of Low (○), High (●), Variable (■) and Field (□) ewes detected in oestrus during February - March 1972 (referred to as March 1972).

Vasectomised rams were joined on 23 February 1972 (day 0).

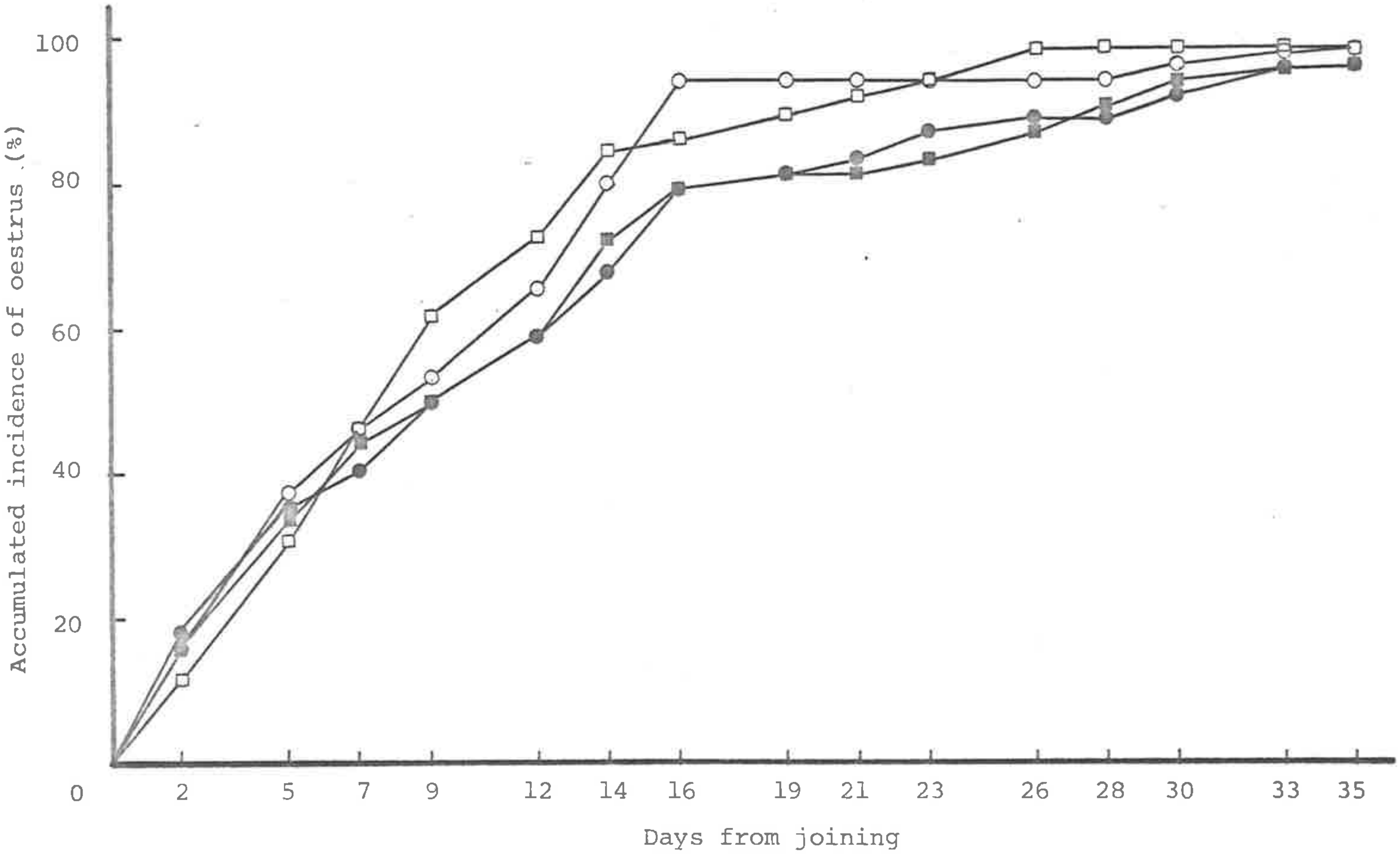

Accumulated incidence of oestrus (%)
100
80
60
40
20
0
2
5
7
9
12
14
16
19
21
23
26
28
30
33
35
Days from joining

Figure 4. The accumulated percentage incidence of Low (○), High (●), Variable (▣) and Field (□) ewes detected in oestrus during August - September 1972 (referred to as September 1972).

The rams were joined on 23 August (day 0).

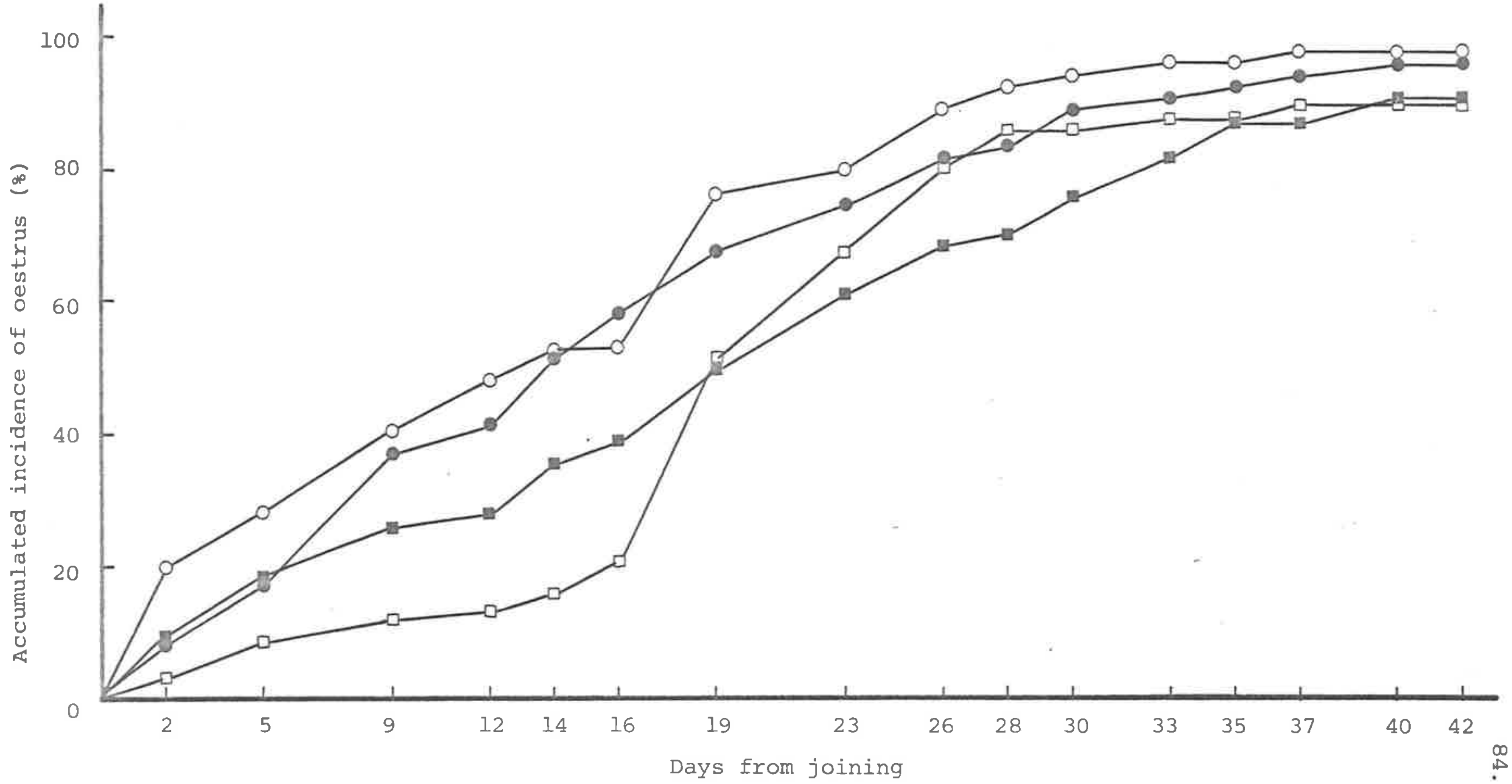
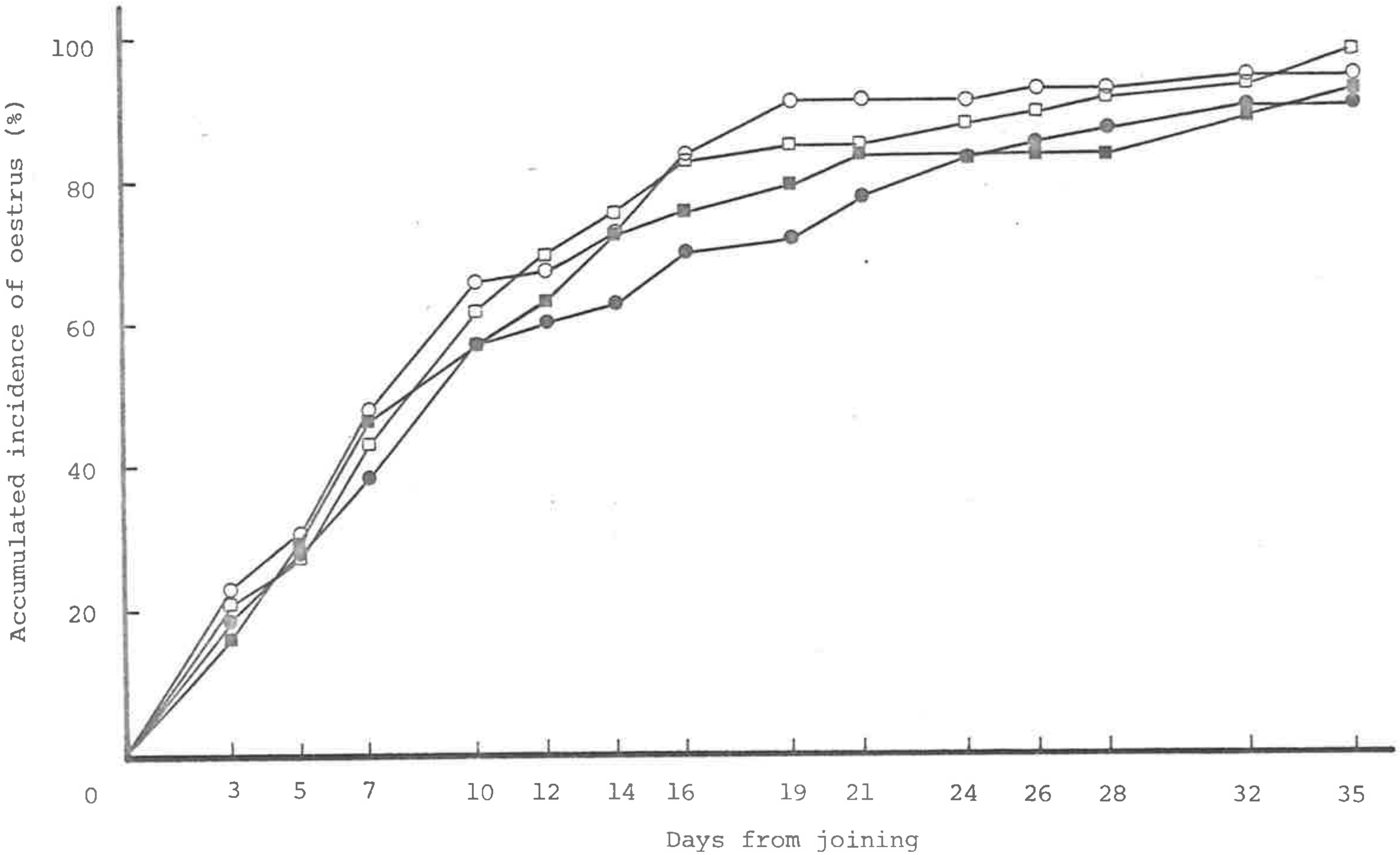

Accumulated incidence of oestrus (%)
100
80
60
40
20
0
2
5
9
12
14
16
19
23
26
28
30
33
35
37
40
42
Days from joining

Figure 5. The accumulated percentage incidence of Low (○), High (●), Variable (■) and Field (□) ewes detected in oestrus during February - March 1973 (referred to as March 1973).

The rams were joined on 16 February (day 0).



Accumulated incidence of oestrus (%)
100
80
60
40
20
0
3
5
7
10
12
14
16
19
21
24
26
28
32
35
Days from joining

Table 2. The incidence of ewes detected in oestrus to (a) day 16 and (b) day 35 after joining for each treatment group at each time of joining. The chi-square value and significance level is shown for the comparison of the four treatment groups at each season.

Time of joining	Treatment group				χ^2_3	Sig.
	Low	High	Variable	Field		
(a) Incidence to day 16						
February - March 1972	53[a]/56[b] (94.6)[c]	43/54 (79.6)	43/54 (79.6)	50/58 (86.2)	6.64	N.S.
September 1972	30/56 (53.5)	31/54 (57.4)	21/54 (38.9)	12/58 (20.7)	19.31	***
February - March 1973	47/56 (83.9)	38/54 (78.4)	41/54 (75.9)	48/58 (82.8)	3.91	N.S.
(b) Incidence to day 35						
February - March 1972	55/56 (98.2)	52/54 (93.8)	52/54 (96.3)	57/58 (98.3)	0.80	N.S.
September 1972	54/56 (96.4)	52/54 (96.3)	47/54 (87.0)	51/58 (87.9)	5.88	N.S.
February - March 1973	53/56 (94.6)	49/54 (90.7)	50/54 (92.6)	57/58 (98.3)	3.19	N.S.

a Number of ewes detected in oestrus
b Total number of ewes in the group
c Percentage of ewes detected in oestrus

*** $P < 0.001$
N.S. Not significant

(b) Effect of time of joining (within treatment group)

The accumulated incidence of ewes detected in oestrus at each of the three times of joining is shown for each treatment group individually in Figures 6, 7, 8 and 9.

It is apparent from these Figures that for each group the pattern of occurrence of oestrus was similar during both sets of observations made in March and that this common pattern was different to that observed in September. The difference in September was least among High ewes, intermediate among Low and Variable ewes and greatest among Field ewes.

Chi-square data relating to the incidence of oestrus to either day 16, or day 35, for comparisons between March 1972, September 1972 and March 1973 (2 d.f.); March 1972 and September 1972 (1 d.f.); September 1972 and March 1973 (1 d.f.) and between March 1972 and March 1973 (1 d.f.) are shown in Table 3 (calculated from data in Table 2). The incidence of oestrus to day 16 was not homogeneous, over the three times of observation, for any of the groups (High, $P < 0.05$; other three groups, $P < 0.001$). A greater incidence was detected in each group during March 1972 than during September 1972 (High, $P < 0.05$; other three groups, $P < 0.001$) and in three groups during March 1973 than during September 1972 (High, not significant; other three groups, $P < 0.001$). Each group performed similarly during March 1972 and March 1973.

The time of joining did not significantly affect the incidence of oestrus detected to day 35 among either the Low, High or Variable groups. However, the incidence among the Field group was affected ($P < 0.01$):

Figure 6. The accumulated percentage incidence of Low ewes detected in oestrus during March 1972 (▼), September 1972 (▽) and March 1973 (▲).

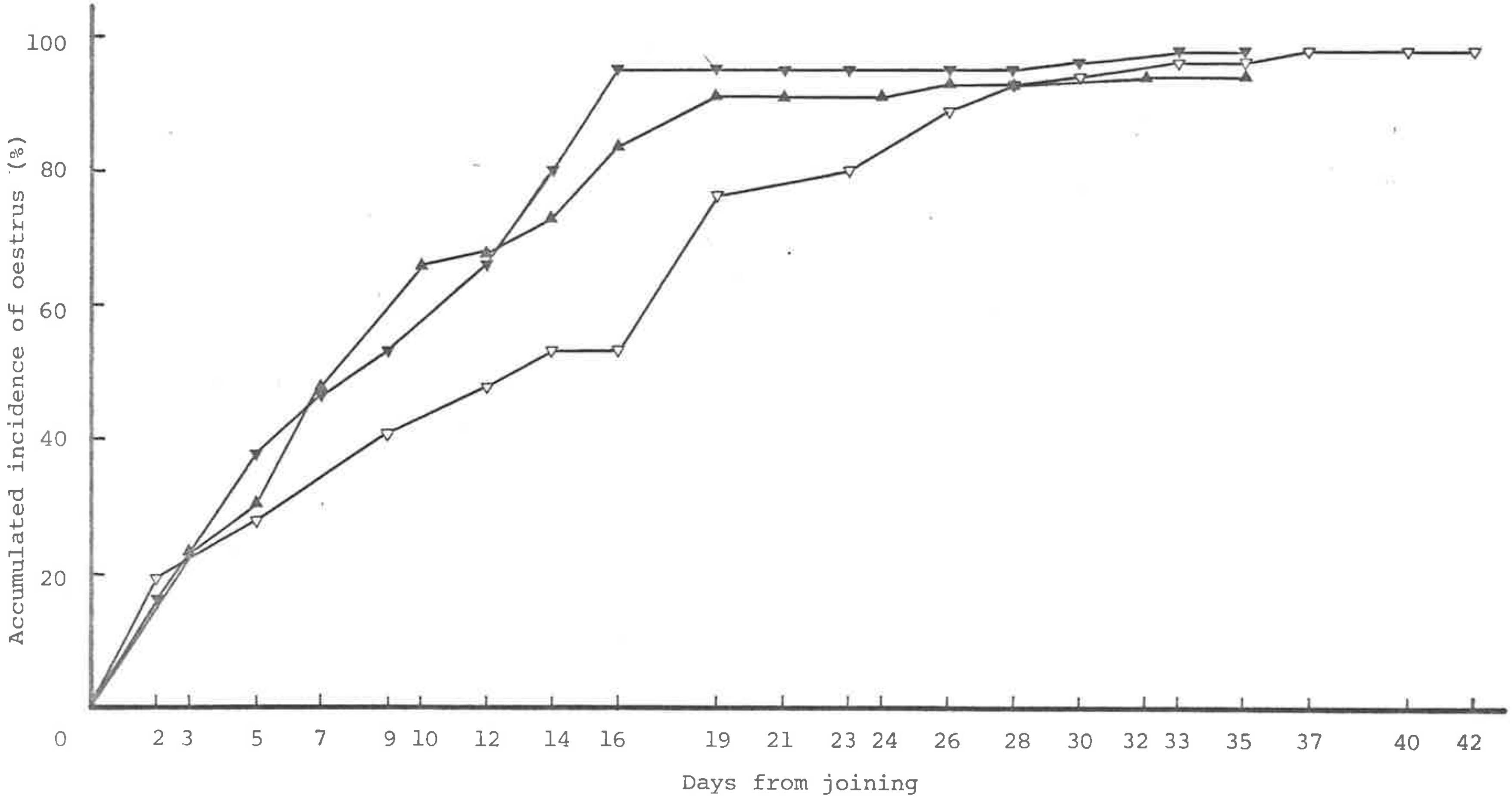

Accumulated incidence of oestrus (%)
100
80
60
40
20
0
2
3
5
7
9
10
12
14
16
19
21
23
24
26
28
30
32
33
35
37
40
42
Days from joining

Figure 7. The accumulated percentage incidence of High ewes detected in oestrus during March 1972 (▼), September 1972 (▽) and March 1973 (▲).

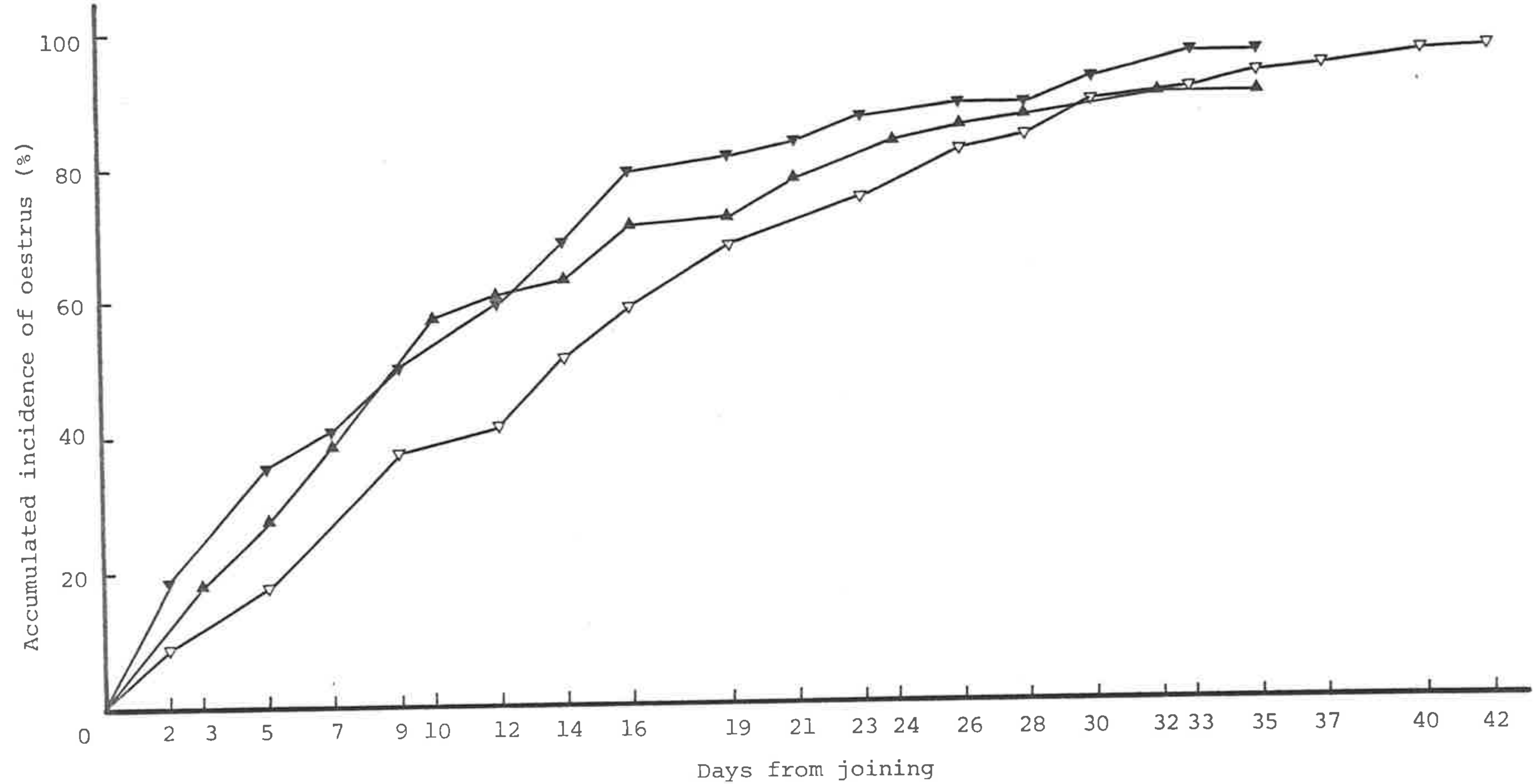

Accumulated incidence of oestrus (%)
100
80
60
40
20
0
2
3
5
7
9
10
12
14
16
19
21
23
24
26
28
30
32
33
35
37
40
42
Days from joining

Figure 8. The accumulated percentage incidence of Variable ewes detected in oestrus during March 1972 (▼), September 1972 (▽) and March 1973 (▲).

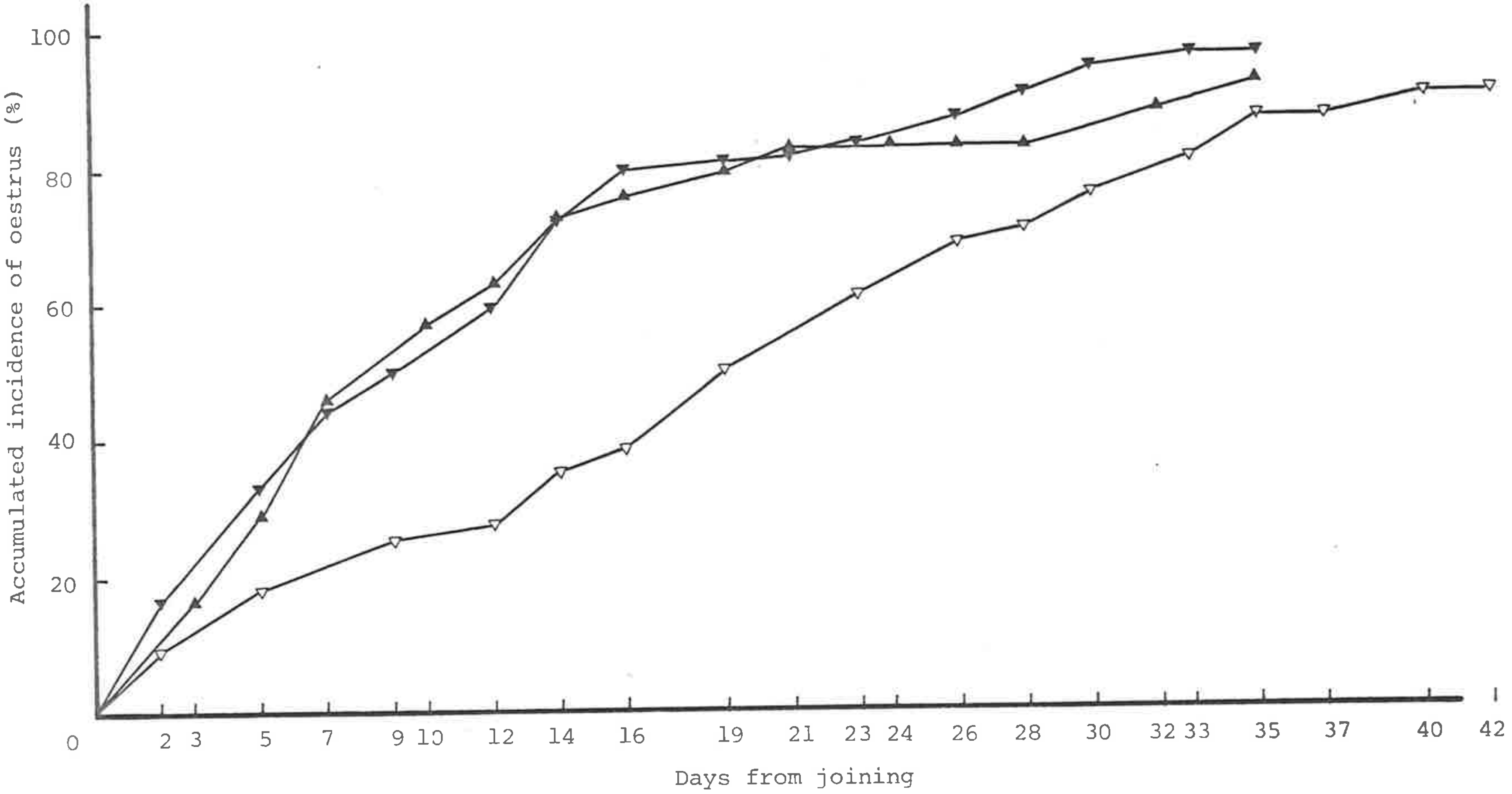

100
80
60
40
20
0
Accumulated incidence of oestrus (%)
2
3
5
7
9
10
12
14
16
19
21
23
24
26
28
30
32
33
35
37
40
42
Days from joining

Figure 9. The accumulated percentage incidence of Field ewes detected in oestrus during March 1972 (▼), September 1972 (▽) and March 1973 (▲).

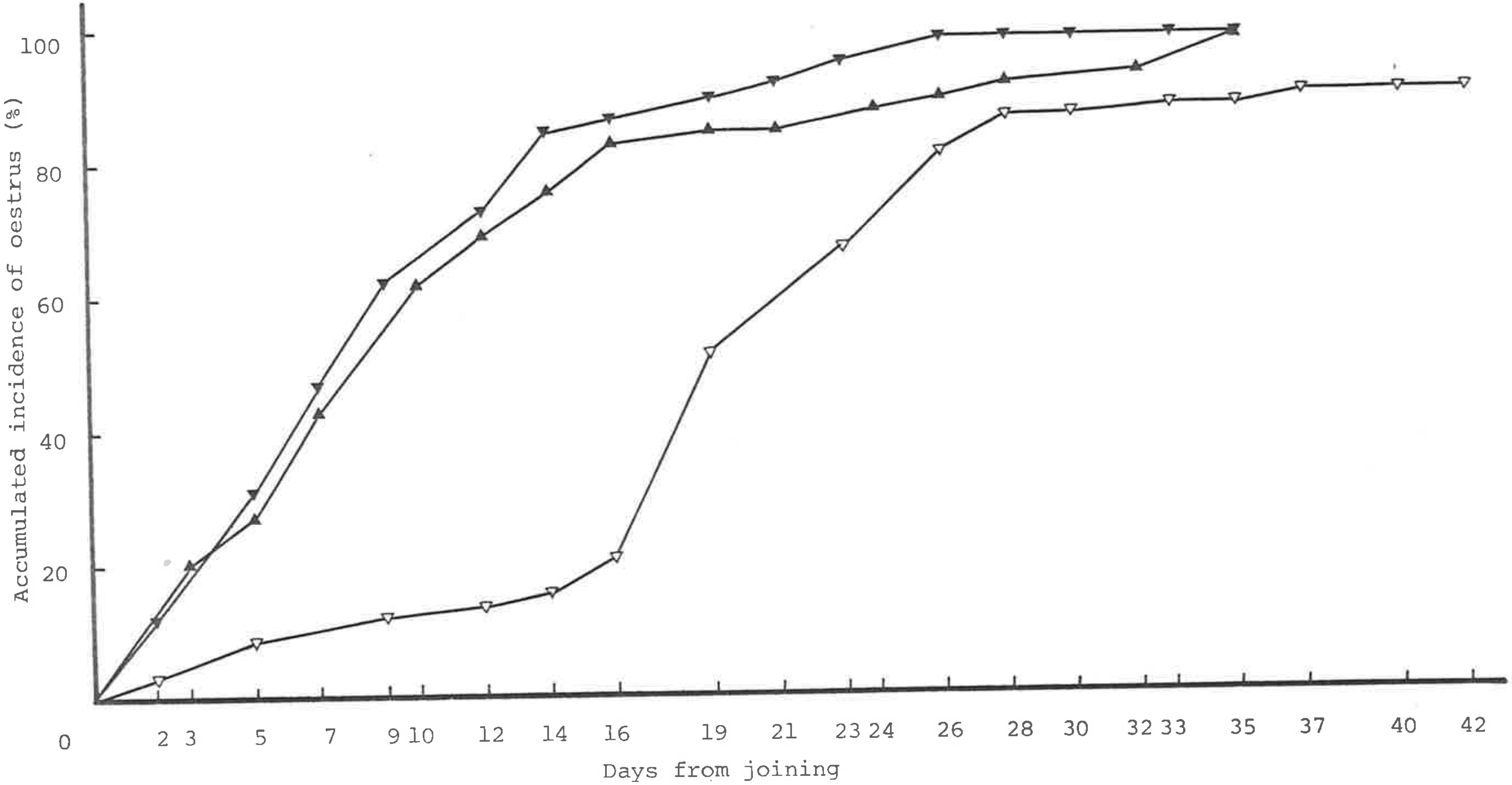

Accumulated incidence of oestrus (%)
100
80
60
40
20
0
2
3
5
7
9
10
12
14
16
19
21
23
24
26
28
30
32
33
35
37
40
42
Days from joining

Table 3. The chi-square value and significance level relating to the accumulated incidence of oestrus for each treatment group when compared at the following combinations of times of joining: (a) March 1972, September 1972, March 1973, (b) March 1972, September 1972, (c) September 1972, March 1973, and (d) March 1972, March 1973.

Times compared	Treatment group			
	Low	High	Variable	Field
(a) *Incidence of oestrus to day 16*				
March 1972 September 1972 March 1973	29.0 ***	6.31 *	24.0 ***	67.8 ***
March 1972 September 1972	24.6 ***	6.18 *	18.6 ***	50.0 ***
September 1972 March 1973	12.0 ***	1.97 N.S.	15.2 ***	44.7 ***
September 1972 March 1973	2.33 N.S.	1.23 N.S.	0.21 N.S.	0.26 N.S.
(b) *Incidence of oestrus to day 35*				
March 1972 September 1972 March 1973	1.04 N.S.	2.12 N.S.	3.18 N.S.	8.44 **
March 1972 September 1972	0.34 N.S.	0.26 N.S.	3.03 N.S.	4.83 * (3.36[a]) N.S.
September 1972 March 1973	0.21 N.S.	1.37 N.S.	0.91 N.S.	4.83 * (3.36[a]) N.S.
March 1972 March 1973	1.04 N.S.	1.37 N.S.	0.71 N.S.	0.0 N.S.

[a] χ_c^2

*	$P < 0.05$
**	$P < 0.01$
***	$P < 0.001$
N.S.	Not significant

there being a lower incidence during September. Chi-square analysis showed the difference between both March 1972 and September 1972, and between September 1972 and March 1973 was significant ($P < 0.05$) but when Yates' Correction for Continuity was applied (necessary because of small expected numbers) the resultant χ_c^2 values were not significant ($P < 0.1$).

(c) Effect of treatment (pooled over all times)

The incidence of oestrus to day 35 was pooled over the three times of joining for each of the three pen-fed groups. The three groups performed similarly ($\chi_2^2 = 3.06$; $P < 0.3$).

Significant effects of time of joining precluded the pooling of data for the Field group for the incidence to day 35, and of each group for the incidence to day 16.

(d) Effect of time of joining (pooled over all treatments)

The incidence of oestrus to day 35 was pooled over the four treatments for each of the times of joining. The pooled incidences of 97.3 per cent (March 1972), 91.9 per cent (September 1972) and 94.1 per cent (March 1973) were not homogeneous. The incidence during September was significantly lower than during March 1972 ($P < 0.05$) but not significantly different to that observed during March 1973.

Significant treatment effects during September 1972 precluded the pooling of data relating to the incidence of oestrus to day 16 except for March 1972 (85.1%) and March 1973 (78.4%) which were not significantly different.

(e) Specific comparisons

Three specific comparisons were made of the effect of conditions experienced during the experiment on the incidence of oestrus to day 16, and day 35. They were those between:

(i) constant low liveweight and constant high liveweight
(ii) constant liveweight and changing liveweight (both in pens), and
(iii) changing liveweight in pens and changing liveweight in the field.

The chi-square value and associated significance level for each of these comparisons, concerning the incidence of oestrus to day 16, are shown in Table 4. A similar set of analyses of the incidence to day 35 indicated that there were no significant differences at that time.

(i) Constant low and constant high liveweight (both in pens)

There was a significantly higher incidence of oestrus to day 16 among Low ewes (94.6%) than among High ewes (79.6%) in March 1972 ($P < 0.05$). While the difference did not reach significance, there was a similar trend again in March 1973 (83.9%, 70.4%). Analysis of pooled data for March 1972 and March 1973 revealed significantly greater incidence among the Low group (89.3%) than among the High group (75.0%) (P   0.01). Both groups performed similarly during September 1972.

(ii) Constant and changing liveweight (both in pens)

The incidence of oestrus to day 16 was significantly higher among Low ewes (94.6%) than Variable ewes both in March 1972

Table 4: Chi-square value and significance level for the incidence of oestrus detected to day 16 at each time of joining for comparisons between (a) constant low and constant high liveweight, (b) constant and changing liveweight (both in pens), and (c) changing liveweight in pens and in the field.

Treatment groups compared	Time of joining							
	March 1972		September 1972		March 1973		March 1972 & 1973	
	X_1^2	Sig.	X_1^2	Sig.	X_1^2	Sig.	X_1^2	Sig.
(a) <u>Constant low and constant high liveweight</u>								
Low/High	5.57	*	0.16	N.S.	2.88	N.S.	7.69	**
(b) <u>Constant and changing liveweight (both in pens)</u>								
Low/Variable	5.57	*	-	-	1.10	N.S.	5.32	*
High/Variable	-	-	3.71	N.S.	-	-	-	-
(c) <u>Changing liveweight pens and in the field</u>								
Variable/Field	0.86	N.S.	4.57	*	0.80	N.S.	1.65	N.S.

*	$P < 0.05$
**	$P < 0.01$
***	$P < 0.001$
N.S.	Not significant

(79.6%) ($P < 0.05$) and in March 1972 and March 1973 combined (Low, 89.3%; Variable, 77.8%) ($P < 0.05$). In September 1972, where the relevant comparison was between the High and Variable groups, the Variable group was again lower, but not significantly (High, 57.4%; Variable 38.9%).

(iii) Changing liveweight in pens and in the field

Similar proportions of the Variable and Field groups were detected in oestrus to day 16 in March 1972, March 1973 and March 1972 and March 1973 combined. In September, however, there was a higher incidence of oestrus among Variable (38.9%) than among Field (20.7%) ewes ($P < 0.05$).

2. DISCUSSION

The effect of treatment and time of joining on the incidence of oestrus was both more marked and more complex to day 16 than to day 35. The incidence to day 16 was not affected by treatment in either March 1972 or March 1973, but in September 1972 it was significantly lower for the Field group than for the other three groups. The influence of time of joining on the incidence of oestrus to day 16 was most marked in the Field group where only 21 per cent of the ewes were detected in oestrus in September compared with 86 per cent and 83 per cent in March 1972 and March 1973, respectively - a depression in incidence of 64 per cent between March and September. The comparable depression for the Variable, Low and High groups was 39 per cent, 38 per cent and 18 per cent, respectively.

The study has shown clearly that the incidence of oestrus to day 35 was not differentially affected by any of the treatments at any one of the three times of joining. However, there was a small overall effect of time of joining with a lower incidence in September than in March. There was a depression in the incidence of oestrus to day 35 between March and September of 10 per cent for the Field group ($P < 0.05$), 8 per cent for the Variable group (n.s.), no difference for the Low group and an elevation of 3 per cent for the High group (n.s.). It seems that there were more Field ewes resolutely anoestrus in September than in March.

(a) Specific comparisons

(i) Low and high constant liveweight

Analysis of the March 1972, and combined March 1972 and 1973, data revealed that there was a greater incidence of oestrus to day 16 among the Low ewes than among the High ewes. This situation is not consistent with the findings of Hafez (1952) or Allen and Lamming (1961). On the basis of their investigations I would have expected either no difference (the present treatments were not as severe) or that the Low ewes would have had the lower incidence.

Additional examination of the present data suggest that the result to day 16 may have been fortuitous or the apparent effect was of a marginal nature. Of the fifteen times (days) that oestrus was recorded during March 1972 (Appendix Table 7) it was only on day 16 that there was a significant difference between the Low and High ewes. In March 1973 there was a difference at day 19 ($P < 0.05$) only and on a pooled basis (March 1972 and 1973) there were differences at days 16 ($P < 0.01$), 19 ($P < 0.001$) and 21 ($P < 0.01$) only.

These additional analyses show that there was a similar pattern of oestrus to day 14, followed by a slight synchronisation of oestrus among Low ewes but not among High ewes. This, combined with an overall tendency towards a lower incidence among High ewes, resulted in the difference observed until day 21. Considered overall, the difference was marginal. An error in the detection of oestrus in two ewes in either group in each year could have been responsible for the difference. On the other hand the similarity in behaviour of each group in both seasons tends to confirm that the observed patterns were an accurate assessment of the behaviour of the particular ewes forming the groups.

In view of the marginal nature of the difference the apparent conflict in behaviour compared with that observed by Hafez (1952) and by Allen and Lamming (1961) should be regarded with caution: although the possibility that a continuing high level of nutrition may depress oestrus cannot be completely dismissed.

The levels of oestrous activity determined under constant liveweight conditions in this study can be compared with those of previous observations on ewes from the same flock (Cutten, unpublished). Relevant information concerning differences in the mean liveweight of the ewes, and both the season and the timing of observing oestrus, are shown in Table 5, together with the comparable data on the incidence of oestrus from the two studies. Apart from one substantially different incidence to day 14 - that of the previously observed group joined on 20 March, 1970 - there was reasonable within-season agreement between the various observations of oestrus in summer/autumn and in winter/spring. The between-season differences were particularly consistent.

Table 5: The incidence of oestrus to both day 14 and day 35, date of observation, mean wool-free fasted liveweight and the total number of animals observed for the Low and High groups of this study and for comparable groups from the same flock studied previously.

Group	Total No. ewes	Liveweight (Kg)	Date[a]	Incidence of oestrus (%) Day 14[b]	Incidence of oestrus (%) Day 35
(a) *Summer/Autumn*					
1972 Low	56	44	23/2/72	80	98
1972 High	54	52	"	69	94
1973 Low	56	44	16/2/73	73	95
1973 High	54	52	"	63	91
Previous	41	49	20/3/70	93	100
Previous	39	49	29/1/71	74	100
(b) *Winter/Spring*					
1972 Low	58	42	23/8/72	54	96
1972 High	58	48	"	51	96
Previous	41	47	31/7/70	54	98
Previous	40	49	21/9/70	58	100

[a] Date on which rams were joined (day 0)

[b] Note that the incidence is to day 14 rather than day 16, as this is how the previous data were recorded

There is no single obvious explanation for the 93 per cent incidence of oestrus to day 14 among the 41 ewes joined on 20 March, 1970. This incidence was higher than could be expected on theoretical grounds even if all of the ewes were cycling when the rams were joined. With an average oestrous cycle length of 17 days and random phasing of the cycles 82 per cent of the flock would be expected to exhibit oestrus in 14 days. Allowing that a ram may detect a ewe that has been in oestrus for 24 hours the expected incidence rises to 88 per cent. It is likely, therefore, that either there was not random phasing of the cycles (i.e. there was some degree of synchronisation at the time of joining), or the rams raddled several non-oestrous ewes, or there were several ewes detected later than 24 hours after coming into oestrus. Four ewes raddled in any of these circumstances, the latter two of which are not unlikely, would have increased the incidence from 82 per cent to 93 per cent - a level not markedly dissimilar to the other levels observed.

The fact that there was reasonable agreement within the seasons of observations despite substantial variations in mean liveweight and some variation in season is not inconsistent with other reported findings. Firstly, the incidence of behavioural oestrus seems to be depressed only under conditions of severely low nutrition, and then possibly only when this is associated with a rapid decline in liveweight (Hafez, 1952; Allen and Lamming, 1961). Neither of these conditions was fulfilled in either the present or the previous study. Secondly, Hafez (1952) and Watson (1952) both postulated that there is a gradual cyclic change in the level of sexual activity during the course of each year. In this circumstance it is reasonable to expect little change in oestrous activity over a six or seven week period; particularly when the period is near the time of either maximum or minimum activity (i.e. the two periods during which the rate of change of activity, with time, is least). The similarlity, within each broad season, of the data summarised in Table 5 is consistent with the views of both Hafez and Watson.

The patterns of oestrous behaviour observed among the Low and High ewes in this experiment conformed with each other and with that observed previously in the same flock. This clearly confirms the ability of almost all Koonoona ewes to exhibit oestrus at any season of the year, when maintained at a constant liveweight on a hay/grain ration. This ability exists over the liveweight range from 45 kg to 54 kg at least. The pattern of occurrence of oestrus has been shown to differ consistently between seasons of expected maximum and minimum oestrous activity.

(ii) Constant and changing liveweight in pens

The nature of the comparison between the Low and Variable groups in March was similar to that of the Low and High groups discussed in (i) above, except that there was not a difference at any day in March 1973, and only at days 16 ($P < 0.05$), 19 ($P < 0.01$), 21 ($P < 0.05$) and 26 ($P < 0.05$) when the data for March 1972 and 1973 were pooled. While the lower incidence of oestrus to day 16 among the Variable ewes was more marked than in the previous comparison the comments made there apply here also (with the exception that an error in the detection of three ewes rather than two would have been necessary).

This experiment did not provide evidence that the seasonal fluctuations in liveweight experienced by the Variable group were associated with a substantially altered pattern of occurrence of oestrus, compared with that exhibited by the ewes maintained at a steady liveweight.

(iii) Changing liveweight in pens and in the field

The interesting observations in this comparison were those made in September 1972 (Figure 4, Appendix Table 7b) when less Field than Variable ewes were detected in oestrus to day 14 ($P < 0.05$) and day 16 ($P < 0.05$) but more to day 28 ($P < 0.05$). The groups clearly exhibited contrasting patterns of oestrus.

The behaviour of the Field ewes can be readily explained in terms of well-established principles of oestrous behaviour involving some ewes that are cycling regularly before joining, some that are stimulated by the sudden association with rams and some that remain anoestrous throughout joining. These principles do not provide a ready explanation for the observed behaviour of the Variable ewes, where there was apparently no ram stimulated synchronisation of oestrus, but fresh ewes were detected in oestrus at a steady rate over the whole period up to day 35.

The abnormal behaviour of the Variable group could be explained by postulating that a significant proportion (50% ?) of the ewes experienced either silent oestrus (ovulation without behavioural oestrus) or oestrous cycles of irregular length and that the oestrous behaviour of these ewes was not influenced by the introduction of rams, or at least not in the classical manner. While the highest reported incidence of silent oestrus appears to be only about 18 per cent over a full breeding season and 35 per cent over a one month period (Hafez 1952) the latter value is sufficient to give a degree of credibility to the hypothesis.

The incidence of oestrus observed to day 16 among the Field ewes during September was not only lower than among the Variable group: it was also lower than among the other two pen-fed groups. This emphasises that the Field ewes did perform differently, and clearly indicates that there could be difficulties in extrapolating the results of pen-feeding experiments to grazing situations. The practical effects are limited, however, and are considered below. While differences in the proximity of rams, or the level of nutritional, or non-nutritional, stress on the various groups could offer an explanation for the lower incidence observed among the Field ewes, none are singly convincing. The three pen-fed groups were located sufficiently distant from the Field group that there could have been a differential ram synchronisation effect prior to joining. This is unlikely to have happened though, as care was taken to keep rams at least 300 metres away from either location at all times except during the joining periods: a distance considered to exclude any effect of rams (Watson and Radford, 1960). As the Variable ewes did not lose as much liveweight during late autumn and early spring, and as undernutrition late in the breeding season has been shown to hasten the onset of the non-breeding season (McKenzie and Terrill, 1937; Smith, 1962), the additional nutritional stress experienced by the Field ewes might have reduced their sexual activity relative to the Variable ewes. However, as the differential loss in weight was not great, and ceased about two months before oestrus was observed in September, it is not likely that there was such an effect on this occasion. This view is supported by the fact that both the Low and High groups had practically the same incidence to day 16 despite larger differences in liveweight, and presumably nutritional stress, than between the Field and Variable groups. While they did not study the effect of close confinement and frequent handling specifically, Doney, Gunn and Griffiths (1973), and Mackenzie, Thwaites and Edey (1975) both found that adverse climatic conditions delayed oestrus. Braden and Moule (1964) studied the effect of handling and transportation stress but mainly in relation to ovulation. They found that ovulation, unaccompanied by oestrus, was stimulated among anoestrous ewes but they did not determine whether the ewes exhibited oestrus a cycle length later (as with ram stimulation). During the breeding season ovulation was delayed among some of the ewes due to ovulate within 0 to 3 days following the stress period. Doney *et al.* (1973) have also reported that climatic stress during the latter part of the oestrous cycle depressed ovulation rate. In view of these reports one would expect that, if there was an effect of confinement, or handling, the pen-fed groups have have had the lower level of oestrous activity, and not the Field group.

(b) Practical implications of different patterns of oestrus

What is the likely effect, on the incidence of barren ewes, of the different patterns of oestrus observed for the pen-fed and grazed ewes? The differences observed in September imply that as many as 30 per cent of the Field ewes would have had one less opportunity to exhibit behavioural oestrus during a given period of joining compared with either the Low or High ewes. If the ewes were joined for five weeks (two oestrous cycles) and 30 per cent of them returned to service after each service (Lindsay, Knight, Smith and Oldham, 1975) it follows that with 30 per cent of the ewes experiencing one less oestrus there should be 6.3 per cent more barren ewes (21% more if joined for only one cycle). If the joining period was extended over three cycle lengths the expected increase would be only 1.9 per cent. These calculated expectations do not allow for either embryo loss after the joining period, or for the ewes stimulated to cycle to cease cycling before the end of joining: such losses would act to reduce the increase.

As there is commonly a 10 per cent to 15 per cent incidence of barren ewes among commercial flocks an increase of 6 per cent is substantial. This experiment clearly indicates that caution should be exercised in extrapolating the behaviour of the pen-fed groups to a commercial situation. In the practical situation the effect could be reduced to a relatively insignificant level (2% or less) simply by ensuring that joining continued for a minimum of three oestrous cycle lengths.

3. SUMMARY

(1) The incidence of oestrus detected to day 16 was significantly affected by the treatments imposed during the season of expected minimum sexual activity (September 1972) but not during the season of expected maximum sexual activity (March 1972, 1973). During September there was a lower incidence among the Field ewes than among each pen-fed group (Low, High, Variable).

The incidence to day 16 was affected by the time of joining. There was a significantly greater incidence among each group during March 1972, and among three groups during March 1973, than during September 1972. The incidence among High ewes was similar in September and March 1973.

(2) The incidence of oestrus detected to day 35 was not significantly affected by the treatments imposed or, with one possible exception, by the time of joining. There was a marginally lower incidence among the Field ewes during September than during March.

(3) There was no substantial evidence that the pattern of occurrence of oestrus among the pen-fed groups was affected by either the level of sustained liveweight or the seasonal fluctuation in liveweight.

There was a marked effect of season on the pattern of oestrus: there being a clearly evident ram synchronisation effect when the ewes were joined in late winter/spring but not when they were joined in late summer/autumn.

The levels of oestrous activity observed among the Low and High groups during the expected seasons of maximum and minimum activity confirmed the activities observed among similar ewes in a previous year.

(4) While the pattern of oestrus observed among the Field group was similar to that of the pen-fed groups during March 1972 and March 1973 it was markedly different during September, when about 30 per cent fewer ewes were detected in oestrus to day 16.

This indicates that during the season of minimum oestrus activity (September) extrapolation of the oestrous behaviour of pen-fed ewes to the field situation could involve a commercially significant under-estimation of the incidence of barren ewes.

OVULATION

B. OVULATION

Statistical analyses were conducted on data relating to 203 ewes present at all three sets of observations (March 1972, September 1972, March 1973). Observations made on 35 ewes in March 1972 (Low, 5; High, 9; Variable, 12; Field, 9), on 20 in September 1972 (Low, 4; High, 6; Variable, 7; Field, 3) and 10 in March 1973 (Low, 3; High, 1; Variable, 4; Field 2) were excluded from the analysis. These ewes either died before the final set of observations or it was not possible to make clear observations of the ovaries at one or more times of observation

Chi-square analyses were used to examine the incidence of anovular ewes (among all ewes), the incidence of multiple ovulations (among ovulating ewes) and the incidence of multiple ovulating ewes (among all ewes).

Relationships between ovulatory performance and both liveweight and body condition were examined using linear regression analysis.

In view of the well established relationship between liveweight at ovulation and ovulatory performance the data were considered in two ways. In the first instance the liveweight differences designed into the experiment were ignored and the possible effects of all treatments and all times of joining were examined. Secondly, only those treatments, or times, where the liveweights were theoretically the same were examined. Theoretically, the Low, Variable and Field groups were of similar liveweight in March while the High, Variable and Field groups were similar in September.

1. RESULTS

(a) Effect of treatment (within time of joining)

The incidence of anovular ewes (among all ewes examined) and the incidence of multiple ovulations (among ovulating ewes) observed in each treatment group, at each time of joining, is shown in Table 6. The significance of the overall effect of treatment at each time of joining is also shown.

The treatments imposed did not affect the incidence of anovular ewes at any one of the three times of joining. Nor was there any difference in incidence among the three groups theoretically at the same liveweight.

The incidence of multiple ovulations was affected by the treatments imposed during both March 1972 ($P < 0.01$) and September 1972 ($P < 0.05$) but not during March 1973 ($P < 0.2$).

In March 1972 the three groups with theoretically similar liveweights were not homogeneous ($\chi^2_2 = 6.24$; $P < 0.05$). There was a lower incidence ($\chi^2_1 = 5.21$; $P < 0.05$) of multiple ovulations among the Variable group (19.6%) than among the Field group (40.7%) but the incidence was similar among the Low and Variable groups and also among the Low and Field groups ($\chi^2_1 = 0.28$ and 3.31, respectively).

The three groups expected to have similar liveweight in September 1972 each had a similar incidence of multiple ovulations ($\chi^2_2 = 3.03$). The pooled incidence among these groups (28.6%) was higher than among the Low group (14.0%) ($\chi^2_1 = 4.20$; $P < 0.05$). The groups expected to be

Table 6: The incidence of anovular ewes (among all ewes examined) and the incidence of multiple ovulations (among ovular ewes) for each treatment at each time of joining. The chi-square value and significance level is shown for the comparison of the four treatment groups at each time.

Time of joining	Treatment group				χ^2_3	Sig.
	Low	High	Variable	Field		
(a) Incidence of anovular ewes (among all ewes)						
March 1972	2[a]/52[b] (3.8[c])	1/50 (2.0)	1/47 (2.1)	0/54 (0.0)	2.04	N.S.
September 1972	2/52 (3.8)	3/50 (6.0)	3/47 (6.4)	5/54 (9.3)	1.32	N.S.
March 1973	0/52 (0.0)	1/50 (2.0)	0/47 (0.0)	0/54 (0.0)	3.08	N.S.
(b) Incidence of multiple ovulations (among ovular ewes)						
March 1972	12[d]/50[e] (24.0[f])	24/49 (49.0)	9/46 (19.6)	22/54 (40.7)	12.54	**
September 1972	7/50 (14.0)	13/47 (27.7)	9/44 (20.5)	18/49 (36.7)	9.14	*
March 1973	16/52 (30.8)	21/49 (42.9)	12/47 (25.5)	24/54 (44.4)	5.51	N.S.

a	Number of anovular ewes
b	Total number of ewes in the group
c	% anovular ewes
d	Number of ewes with multiple ovulations
e	Number of ewes ovulating
f	% ovular ewes with multiple ovulations
*	$P < 0.05$
**	$P < 0.07$
N.S.	Not significant

of similar liveweight in March 1973 were homogeneous ($\chi^2_2 = 4.36$).

(b) Effect of time of joining (within treatment groups)

Chi-square values relating to within-treatment comparisons between times of joining are shown in Table 7, both for the incidence of anovular ewes and for the incidence of multiple ovulations.

The incidence of anovular ewes among the Low, High and Variable groups was unaffected by the time of joining. The Field group was affected, although the effect was significant ($P < 0.01$) only when the three times were compared together. The two individual comparisons of March with September were not significant.

The incidence of multiple ovulations was similar at each of the three times of joining for each treatment group. Paired comparisons between times, on a within-group basis, showed that there was a higher incidence of multiple ovulation in the High ewes in March 1972 (49.0%) than in September (27.7%) ($P < 0.05$). There was also a higher incidence among the Low ewes in March 1973 (30.8%) than September (14.0%) ($P < 0.05$).

(c) Effect of treatment (pooled over all times)

The pooled incidence of anovular ewes was similar for the High (3.3%), Variable (2.8%) and Low (2.6%) groups ($\chi^2_2 = 0.16$). Data for the Field group could not be pooled as there was a significant effect of time of joining in that group.

Pooled data for the incidence of multiple ovulations showed a marked effect of treatment ($\chi^2_3 = 60.5$; $P < 0.001$). Comparisons between

Table 7: The chi-square value (and significance level) for the incidence of anovular ewes, and multiple ovulations, for each treatment group when compared at the following combinations of times of joining: (a) March 1972, September 1972, March 1973, (b) March 1972, September 1972, (c) September 1972, March 1973, and (d) March 1972, March 1973.

Times compared	Treatment group Low	 High	 Variable	 Field
(a) Incidence of anovular ewes (among all ewes)				
March 1972, September 1972, March 1973	2.05 N.S.	1.66 N.S.	3.60 N.S.	10.30 **
March 1972, September 1972	0.0 N.S.	0.26 N.S.	0.26 N.S.	3.35 N.S.
September 1972, March 1973	0.51 N.S.	0.26 N.S.	1.38 N.S.	3.35 N.S.
March 1972, March 1973	0.47 N.S.	0.0 N.S.	0.0 N.S.	0.99 N.S.
(b) Incidence of multiple ovulations (among ovular ewes)				
March 1972, September 1972, March 1973	4.08 N.S.	4.08 N.S.	0.56 N.S.	0.63 N.S.
March 1972, September 1972	1.62 N.S.	4.60 *	0.01 N.S.	0.17 N.S.
September 1972, March 1973	4.10 *	2.42 N.S.	0.33 N.S.	0.63 N.S.
March 1972, March 1973	0.59 N.S.	0.37 N.S.	0.47 N.S.	0.15 N.S.

* $P < 0.05$

** $P < 0.01$

N.S. Not significant

pairs of treatments showed that the Field (40.8%) and Variable (21.9%) groups (χ^2_1 = 11.97; P < 0.001) and the High (40.0%) and Low (23.0%) groups (χ^2_1 = 9.94; P < 0.01) were significantly different but that the High and Field groups were similar, as were the Low and Variable groups.

(d) Effect of time of joining (pooled over all treatments)

As there was no effect of treatment on the incidence of anovular ewes it was possible to pool the data within each time of joining. The pooled incidences of 2.0 per cent in March 1972, 5.9 per cent in September 1972 and 0.5 per cent in March 1973 were not homogeneous (χ^2_2 = 13.4%; P < 0.01). The incidence was significantly smaller in both March 1972 (P < 0.05) and March 1973 (P < 0.05) than in September 1972. The incidence was similar in March 1972 and March 1973.

Multiple ovulation data could not be pooled as the treatments were heterogeneous in both March 1972 and September 1972.

(e) Specific comparisons

Three specific comparisons were made of the effect of conditions experienced during the experiment on the incidence of both anovular ewes and multiple ovulations. They were those between:

(1) constant low liveweight and constant high liveweight,
(2) constant liveweight and changing liveweight (both in pens), and
(3) changing liveweight in pens and changing liveweight in the field.

The chi-square value and associated significance level for the incidence of multiple ovulation for each of these comparisons (calculated from data shown in Table 6) is shown in Table 8. A similar set of

Table 8: Chi-square value (and significance level) for the incidence of multiple ovulations at each time of joining for comparisons between (a) constant low and constant high liveweight, (b) constant and changing liveweight (both in pens), and (c) changing liveweight in pens and in the field.

Treatment groups compared	Time of observation March 1972		September 1972		March 1973		March (1972 & 1973)	
	χ^2_1	Sig.	χ^2_1	Sig.	χ^2_1	Sig.	χ^2_1	Sig.
(a) Constant low and constant high liveweight								
Low/High	6.67	**	2.67	N.S.	1.59	N.S.	7.35	**
(b) Constant and changing liveweight (both in pens)								
Low/Variable	0.28	N.S.	-	-	0.33	N.S.	0.61	N.S.
High/Variable	-	-	0.64	N.S.	-	-	-	-
(c) Changing liveweight in pens and in the field								
Variable/Field	5.81	*	2.98	N.S.	3.92	*	9.01	**

*	$P < 0.05$
**	$P < 0.01$
N.S.	Not significant

analyses of the incidence of anovular ewes did not reveal any instances of significant difference.

(i) Constant low and constant high liveweight

There was a higher incidence of multiple ovulations among High ewes than among Low ewes at each of the three times of joining, but the difference was significant in March 1972 only ($P < 0.01$). Analysis of the pooled data for March 1972 and March 1973 also indicated a higher incidence ($P < 0.01$) among the High ewes (45.9%) than among the Low ewes (27.5%).

(ii) Constant and changing liveweight (both in pens)

There were no significant differences among these comparisons.

(iii) Changing liveweight in pens and in the field

There was a higher incidence of multiple ovulations among Field ewes than among Variable ewes at each of the three times of joining, but the difference was significant only in March 1972 ($P < 0.05$) and March 1973 ($P < 0.05$). Analysis of the pooled data for March 1972 and March 1973 also showed that there was a higher incidence ($P < 0.01$) among the Field ewes (42.6%) than among the Variable ewes (22.6%).

(f) Adjustment for difference in liveweight

Differences in mean wool-free, fasted, liveweight have not so far been considered when comparing the incidence of multiple ovulations. However, in view of the established relationship between liveweight at joining and ovulation (established both in this experiment - see following sub-section (g) - and others) these differences need to be considered.

Accordingly, adjustments were considered on the basis of the significant relationship found in this experiment, namely, an increase of 2.18 per cent in the incidence of multiple ovulations for each kilogram increase in liveweight. Adjusted incidences were calculated to the nearest whole number and then examined by chi-square analysis as before. With several exceptions, the corrections acted further to emphasise the difference, or similarity, already identified. The effects of the adjustments were as follows.

(i) Effect of treatment (within time of joining)

Allowance for the Variable group being 1.5 kg heavier in mean liveweight than the other two groups of theoretically similar liveweight in March 1972 (2 fewer multiple ovulations expected out of 46 ewes ovulating) increased the already significant difference in the incidence of multiple ovulations between the three groups (although the significance level remains the same). Corrections for the Variable group being 4 kg lighter in September (4 more ovulations out of 44 ewes) and for the low group being 3 kg lower in March (3 more ovulations out of 52 ewes) both further reduced already non-significant differences.

(ii) Effect of time of joining (within treatment)

Allowance for difference in liveweight were made for the Low group in September 1972 (1.2 kg, increase incidence by 1 in 50), the High group in September 1972 (1.1 kg, increase incidence by 1 in 47) and March 1973 (-0.7 kg, decrease incidence by 1 in 49), the Variable group in March 1972 (1.7 kg, increase incidence by 2 in 46) and the Field group in March 1972 (3.4 kg, increase incidence by 4 in 54). Each adjustment further reduced an already non-significant difference in the incidence of multiple ovulation except for the Field group where there was simply a change in sign. The two paired comparisons previously significant, namely, the Low group in September 1972 and March 1973, and the High group in March 1972 and September 1972 were no longer significantly different (χ^2_1 = 3.09 and 3.69).

(iii) Specific comparisons

Corrections are not appropriate for comparisons between the Low and High groups as they were expected to have different mean liveweights.

Each comparison between the constant liveweight groups and the Variable group is only marginally changed. All differences remain non-significant at the 5 per cent probability level.

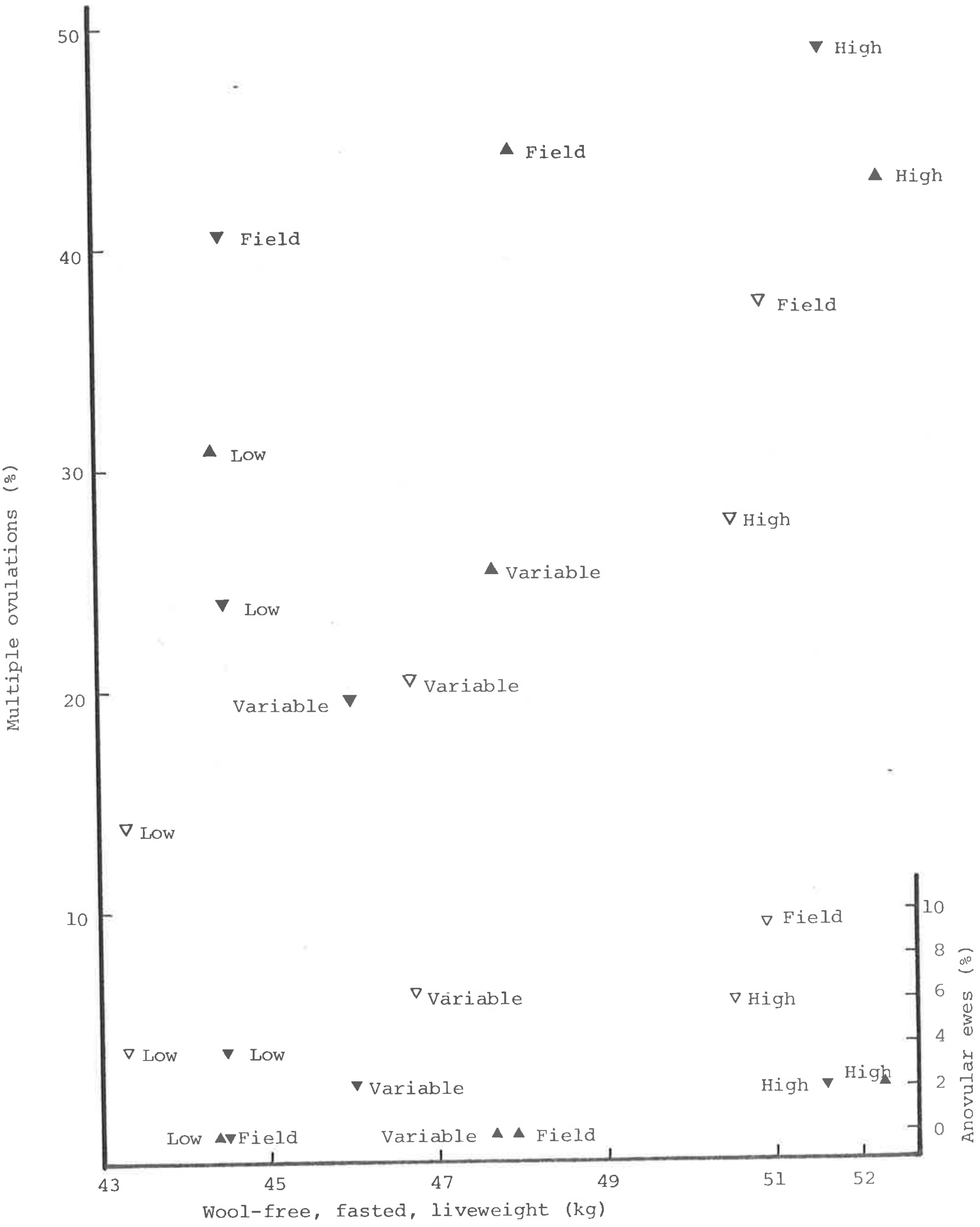
The level of significance of the difference between the Variable and Field groups in March 1972 was altered from the 5 per cent level to the 1 per cent level. Correction for the difference in September further reduced a non-significant difference, while liveweights were already equal in March 1973.

(g) Wool-free, fasted liveweight and body condition index

The relationship between the incidence of both anovular ewes and multiple ovulations, and the group wool-free, fasted liveweight (of ovular and anovular ewes combined) is displayed in Figure 10. Similar relationships but with body condition index are shown in Figure 11.

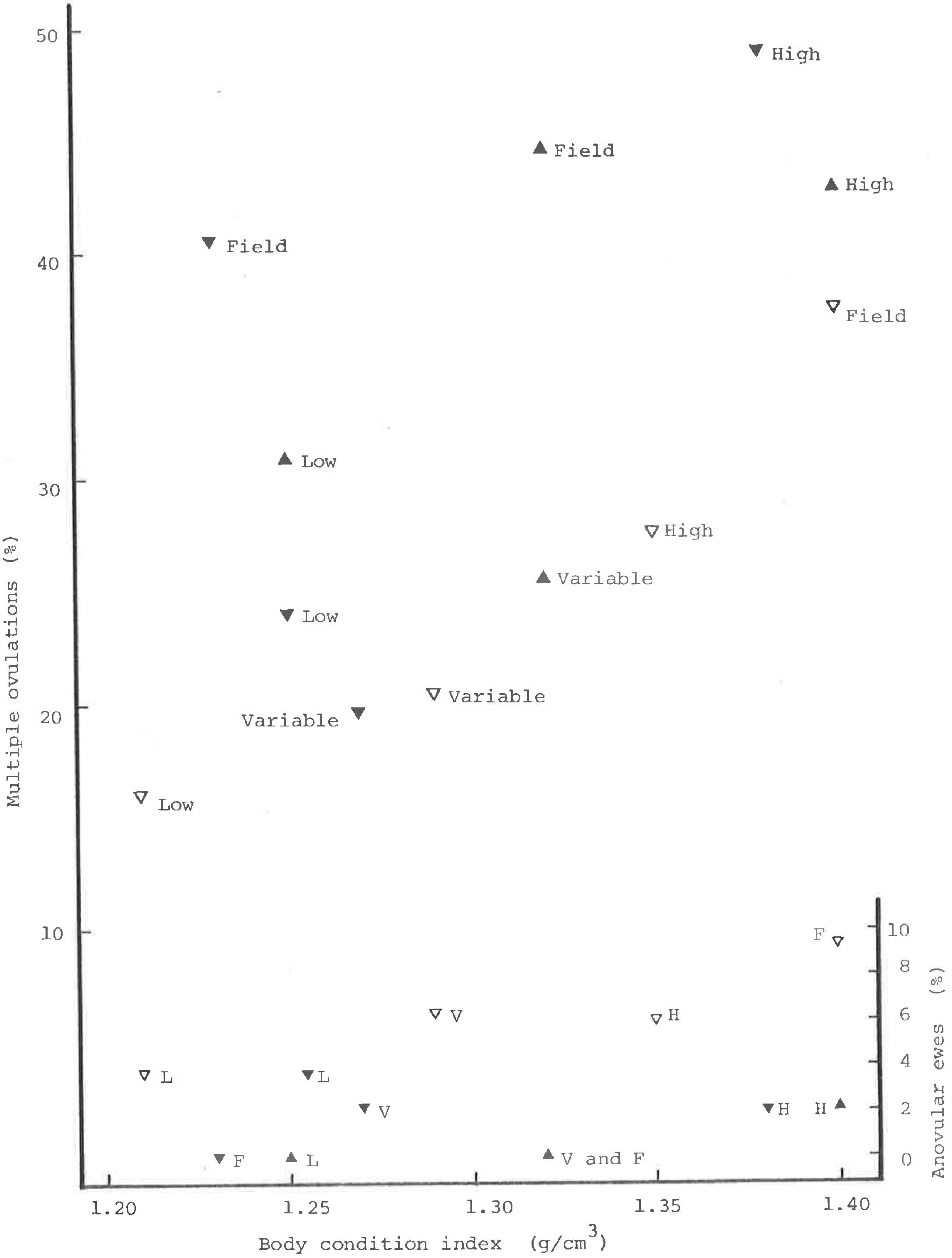
The incidence of anovular ewes was small and variable in both March 1972 and March 1973 and does not appear to have been related to either mean liveweight or body condition index. As noted previously the overall incidence was greater in September 1972. While the data

Figure 10. Relationship between the mean wool-free, fasted, liveweight (kg) of all ewes in the group and the percentage incidence of anovular ewes (per ewe present), and of multiple ovulations (per ewe ovulating), for each group at each time of joining. March 1972 (▼), September 1972 (▽) and March 1973 (▲).



50
40
30
20
10
Multiple ovulations (%)
▼ High
▲ Field
▲ High
▼ Field
▽ Field
▲ Low
▽ High
▲ Variable
▼ Low
▽ Variable
Variable ▼
▽ Low
▽ Field
▽ Variable
▽ High
▽ Low
▼ Low
▼ Variable
High ▼
High ▲
Low ▲▼ Field
Variable ▲ ▲ Field
10
8
6
4
2
0
Anovular ewes (%)
43
45
47
49
51
52
Wool-free, fasted, liveweight (kg)

Figure 11. Relationship between the mean body condition index (g/cm^3) of all ewes in the group and the percentage incidence of anovular ewes (per ewe present), and of multiple ovulations (per ewe ovulating), for each group at each time of joining. March 1972 (▼), September 1972 (▽) and March 1973 (▲).


Multiple ovulations (%)
50
40
30
20
10
High
Field
High
Field
Field
Low
High
Variable
Low
Variable
Variable
Low
F
V
H
L
L
V
H
H
F
L
V and F
10
8
6
4
2
0
Anovular ewes (%)
1.20
1.25
1.30
1.35
1.40
Body condition index (g/cm3)

depicted in Figures 10 and 11 suggest that the incidence then could have increased with increasing liveweight, or body condition index, neither linear regression was significant, although both had a probability of less than 10 per cent.

Linear regression analysis revealed the following significant relationships between the incidence of multiple ovulations (y) and mean wool-free, fasted, liveweight (x).

* All treatments, all times,

$y = 2.18x - 72.1$ 11 d.f.; $P < 0.05$; 36.6% variation explained

* Excluding Field treatment,

$y = 2.74x - 101.7$ 8 d.f.; $P < 0.01$; 64.0% variation explained

* Excluding Field and September,

$y = 2.82x - 103.0$ 5 d.f.; $P < 0.05$; 70.4% variation explained

There was also significant relationships between the incidence of multiple ovulations (y) and mean body condition index (x).

* All treatments, all times,

$y = 100.0x - 99.3$ 11 d.f.; $P < 0.05$; 34.7% variation explained

* Excluding Field treatment,

$y = 142.3x - 157.1$ 8 d.f.; $P < 0.01$; 66.5% variation explained

* Excluding Field and September,

$y = 1.44.1x - 157.1$ 5 d.f.; $P < 0.05$; 67.9% variation explained

It was not possible to examine the data for differences in regressions between times of joining as there was a significant relationship at only one time, namely, between multiple ovulations and body condition index in

September 1972 ($y = 119.7x - 132.3$; $P < 0.05$; 96.2% variation explained). However, it appears in both Figure 10 and Figure 11 that the incidence of multiple ovulations was consistently lower in September than in March. The slope of the relationships appears to have been similar in both March and September.

2. DISCUSSION

(a) Incidence of anovular ewes

The treatments imposed did not significantly affect the incidence of anovular ewes observed at any of the three times of joining. However, with the small numbers of anovular ewes involved, differences of 8 to 10 per cent were required to obtain a statistically significant effect. In this situation there could have been an undetected effect of biological and commercial significance. For example, if it was a true difference, the 5.5 per cent greater incidence among the Field group than among the Low group in September 1972 would be of commercial significance.

The time of joining affected the incidence of anovular ewes, both for the Field group alone and for all of the treatments combined. While the Field group was the only group to have a significantly higher incidence in September than in March each of the other groups showed a similar trend. The overall higher incidence of anovular ewes in September compared with March was not unexpected. For, while they did not refer specifically to anovular ewes, both Hafez (1952) and Watson (1952) concluded that the level of sexual activity of ewes undergoes a cyclic change during the course of each year and is lower in late winter/spring than in autumn.

The higher incidence observed in the present experiment during September was generally consistent with observations of Radford (1959) who found a small incidence of anovular ewes in November and January but not in March, May or August. On the other hand it contrasted with the observed incidences in the previous experiment I conducted, wherein no anovular ewes were observed at any of the eight times of the year except during June/July when there was an incidence of 2.5 per cent.

Although there is no readily identifiable explanation, the finding that the performance of the Field group was significantly affected by the time of joining, while the other groups were not, is not unexpected, as many variables could have been controlled, or altered, by the conditions imposed in the pen situation.

The liveweight level maintained throughout the experiment (Low, High) did not significantly affect the incidence of anovular ewes. Nor was the incidence significantly affected by either seasonal variation in liveweight (compared with steady liveweight) or by grazing in the field (compared with experiencing nutritional condition that resulted in similar liveweight fluctuations while being fed in pens).

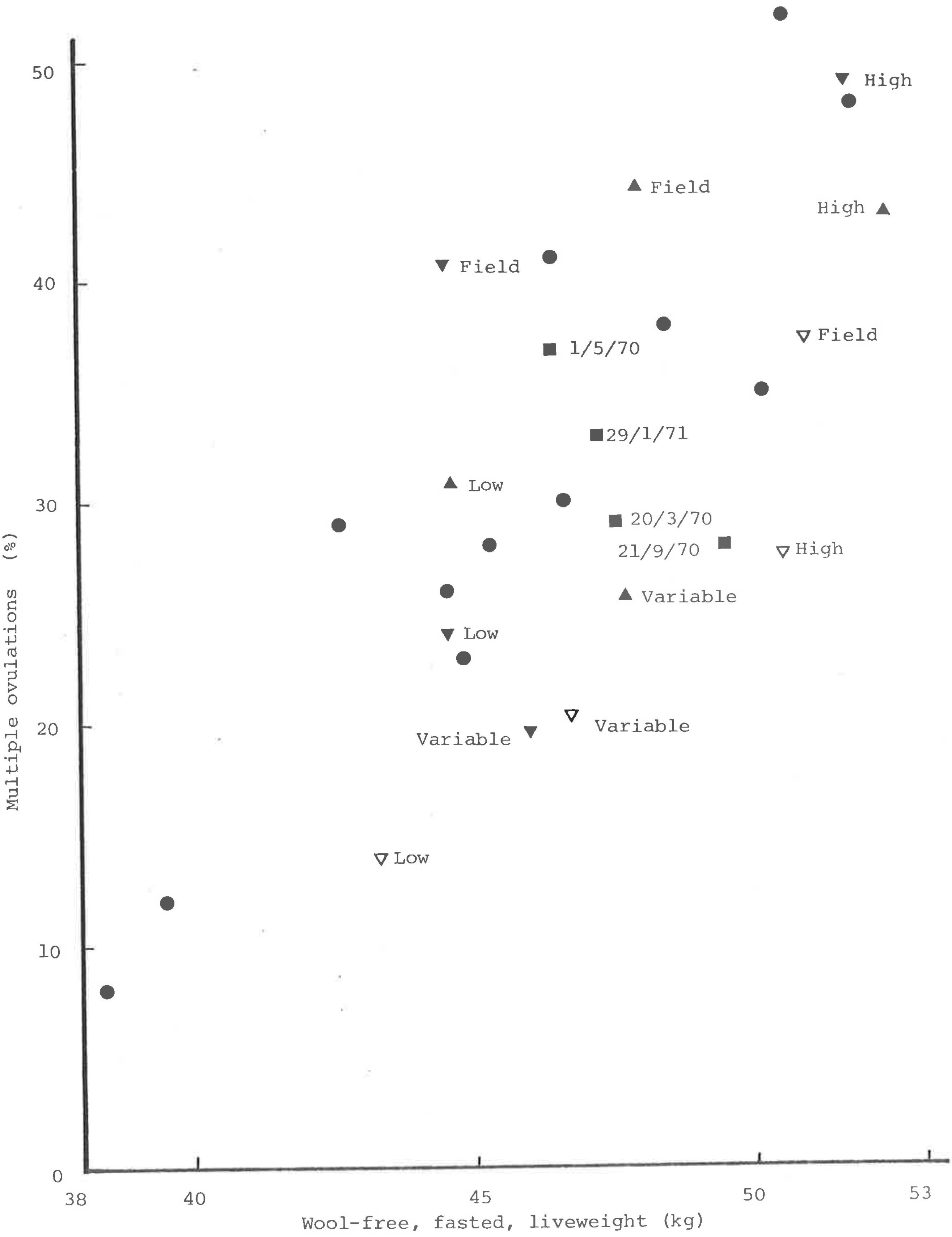
In summary, the incidence of anovular ewes was affected by the time of joining with a higher incidence occurring during September than March. The Field ewes were possibly more severely affected than the other groups. At each time of joining the performance observed under field conditions was similar to that observed under controlled (pen) conditions.

(b) Incidence of multiple ovulations

The study has clearly shown that the incidence of multiple ovulations, observed at comparable mean liveweight in the pen situation, was unaffected by whether the ewes were subjected to an annual cycle of weight change or whether they were maintained at a constant liveweight. Fletcher (1971) has reported a similar finding during autumn. He found that the incidence of multiple ovulations was not influenced by changes in liveweight over a five week period leading up to ovulation. There was one exception, namely, the situation where liveweight decreased to the point that the animals were in an emaciated condition. In this situation the incidence was higher than expected, and was better related to the liveweight of several weeks before ovulation. While, in the present experiment, liveweight declined prior to the March 1973 observations the decline was not as rapid, and the liveweight did not fall as low as in Fletcher's experiment. At the rate and level experienced the findings were in accord with those of Fletcher.

The performance of the High and Low groups during autumn was comparable with that of similar ewes examined by Fletcher (1971). The performances he observed can be compared with the present observations made in autumn (March 1972, March 1973) by reference to Figure 12. The respective performances were very similar. The performances, in both autumn and spring, were also similar to those observed in my previous experiment, wherein ewes with an average weight of 49 kg had an incidence of 29 per cent and 37 per cent during late summer and early autumn and 17 per cent and 27 per cent during early and late spring, respectively.

Figure 12. Relationships between the mean wool-free, fasted, liveweight (kg) of all ewes in the group and the incidence of multiple ovulations (per ewe ovulating) as observed in this study. (March 1972 - ▼, September 1972 - ▽, March 1973 - ▲), by Fletcher (1971) (●) and previously by Cutten (unpublished) (■, date of joining).


Multiple ovulations (%)
0
10
20
30
40
50
Wool-free, fasted, liveweight (kg)
38
40
45
50
53
High
High
Field
Field
Field
1/5/70
29/1/71
20/3/70
21/9/70
Low
Low
Low
High
Variable
Variable
Variable

Fletcher, Geytenbeek and Allden (1970) in their study of maiden first-cross Border Leicester x Merino ewes concluded that there was an interaction between the level of nutrition (liveweight) and the season of joining, with a bigger response to season being displayed by ewes on a higher level of nutrition. This particular point could be considered in the present experiment as there were almost identical differences in liveweight between the Low and High groups at each of the three times of joining. The evidence was equivocal, with an apparent interaction between March 1972 and September 1972 but not between March 1973 and September 1972.

During autumn the Field ewes appear to have behaved differently, both when compared directly with their pen-fed counterparts (Variable ewes), and when compared by regression analysis, on the basis of either liveweight or body condition index, with all the pen-fed groups. Direct comparison of the Field and Variable groups shows that the ewes grazing in the field out-performed their pen-fed counterparts during autumn but not during spring. The performance of the Variable ewes in March 1972 might have been depressed by a carry-over effect of the severe under-nutrition experienced at the beginning of the experiment. However, the similar difference in March 1973 cannot be attributed to severe under-nutrition, nor to differences in liveweight at ovulation as allowance for small differences in weight emphasises the ovulatory difference, as has been pointed out previously. Consideration of the regression relationships between the incidence of multiple ovulation and either wool-free, fasted liveweight or body condition index both point to the Field group performing better than expected compared with the pen-fed groups: the point of interest being that each relationship was improved by exclusion of the Field data. Clearly the greater incidence of multiple ovulation observed among the Field ewes during autumn cannot be explained on the basis of either liveweight or body condition. During spring the incidence appears to have been better related to body condition index than to liveweight.

Between group differences in the body components of fat, protein or water may offer an explanation for the different ovulatory response observed among the Field ewes. Season and treatment differences in these factors are considered in the next section, and discussed in relation to ovulation in the General Discussion chapter.

3. SUMMARY

(1) The incidence of anovular ewes was not significantly affected by the treatments imposed at any of the three times of joining. The incidence among the Field ewes, and among all ewes, was significantly higher in spring than in autumn.

Neither the level of sustained liveweight, the annual cycle of liveweight change, nor the field grazing conditions significantly affected the incidence of anovular ewes.

The incidence of anovular ewes observed in this study was greater in both autumn and spring (about 4% and 7% respectively) than in a previous study of similar ewes (0% and about 3% respectively).

As the incidence of anovular ewes was low the sensitivity of the statistical analysis was such that commercially significant differences could have remained undetected.

(2) The treatments imposed affected the incidence of multiple ovulations observed during March and September 1972, but not during March 1973. There was no significant within-treatment effect of time of joining.

There was consistently a higher incidence among the High ewes than among the Low ewes, although the difference was significant only in autumn (March 1972, March 1972 and March 1973 combined). When considered in relation to liveweight at ovulation the different levels of incidence were comparable with previous observations of similar ewes.

There was no evidence, within the pen-fed groups, that an annual cycle of weight change affected the performance of the ewes relative to that of ewes maintained at a steady liveweight.

The ewes grazed under field conditions had a significantly higher incidence of multiple ovulations in autumn than their pen-fed counterparts that also experienced an annual cycle of liveweight change. Both groups had a similar incidence in spring. The higher incidence among the Field ewes cannot be explained on the basis of either wool-free, fasted, liveweight, or body condition index, at ovulation.

(3) There was a significant linear regression relationship between the incidence of multiple ovulations (y) and both mean wool-free, fasted liveweight (LW) and body condition index (BCI). Based on all observations (4 treatments by 3 times) the regressions were

$$y = 2.18 \text{ LW} - 72.1 \quad (P < 0.05; \; 36.6\% \text{ variation explained})$$

and

$$y = 100.0 \text{ BCI} - 99.3 \quad (P < 0.05; \; 34.7 \text{ variation explained}).$$

The precision of the regression was improved by the exclusion of the Field data to give

$y = 2.74\ \mathrm{LW} - 101.7$ ($P < 0.01$; 64.0% variation explained)

and

$y = 142.3\ \mathrm{BCI} - 157.1$ ($P < 0.01$; 66.5% variation explained)

(4) Although there appeared to be a generally higher incidence of multiple ovulation during March than during September the slope of the regression relationship with both liveweight and body condition index appeared to be similar at both times, i.e. there was no interaction apparent.

BODY COMPOSITION AND WATER TURNOVER

C. SEASONAL VARIATION IN BODY COMPOSITION AND WATER TURNOVER

Body composition estimates were made of 21 ewes in each treatment group at each of nine Times during the course of the experiment (referred to as Time 0 to Time 8, see Table 1). The equations derived by Searle (1970a) were used to estimate water, lean, protein and fat from measurements of tritiated water space and fasted liveweight. The rate of water turnover was measured also on each of these occasions. As the main purpose for making the measurements was to determine the seasonal pattern of change in composition and turnover, those ewes for which there were incomplete sets of data were excluded from the analysis. There were 14 incomplete sets of data (Low, 3; High, 3; Variable, 5; Field, 3).

The variances of the four treatment groups within each Time of observation were examined for homogeneity using Bartlett's test (Steele and Torrie, 1960; page 349). There was a significant level of heterogeneity at Time 5 (December) for fat, % water, % lean, % protein, % fat (each $P < 0.01$) and at Time 8 (February) for water, lean, fat, % protein (each $P < 0.01$) and protein, % water, % lean, and % fat (each $P < 0.05$).

The variances for water turnover were heterogeneous at Times 2, 3, 4 ($P < 0.001$) and 8 ($P < 0.05$). These instances of heterogeneity were ignored in conducting a single way analysis of variance for unequal sub class numbers (Steele and Torrie, 1960; page 112). The variances of the nine Times within each treatment were also tested for homogeneity. Although there was a significant level of heterogeneity in both the High ($P < 0.01$) and Field groups ($P < 0.05$) for % water, % lean, % protein and % fat, and in the Low, Field ($P < 0.001$) and High groups ($P < 0.01$)

for water turnover, these situations were ignored in applying Duncan's multiple range test (Steele and Torrie, 1960; page 107). Variances of the absolute data (i.e. not percentage data) were homogeneous.

1. RESULTS

(a) Mean wool-free, fasted, liveweight

The mean wool-free, fasted, liveweight of the ewes in each treatment group at each of the nine Times of observation is shown in Figure 13. Duncan's multiple range test indicated that the mean liveweight of the Low group was similar at each of the nine Times of observation. The High group was similar at all Times other than Time 0 when it was significantly lower. The mean weight of the Variable group was greater at Times 6 and 7 than at Time 2, and at Time 6 than at Times 0, 1, 2 and 3. The Field group was heavier at Times 5 and 6 than at Times 0 and 7, which in turn were heavier than Times 1, 2 and 8. The significance level for the effect of treatment at each Time of observation is shown in Figure 13.

(b) Estimates of body components

The estimated mean weight of water for each group at each Time of observation is shown in Figure 14. Similar sets of estimates for lean, protein and fat are shown in Figures 15, 16 and 17, respectively. The data for water, lean, protein, and fat, each as a percentage of mean wool-free, fasted liveweight, are shown in Figures 18, 19, 20 and 21, respectively.

(c) Seasonal pattern of change in body components

The equations used to calculate the weight of water

Figure 13. The mean wool-free, fasted liveweight (kg) of the Low (○), High (●), Variable (■) and Field (□) group at each Time of observation (Times 0 to 8).

The significance of the difference between individual treatments, and of all treatments, is shown for each Time of observation. Within each Time, treatments having the same letter are not significantly different; treatments with different letters differ at the 5%, or lower, level of significance; and the overall level of significance is indicated by standard notation (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; N.S., not significant).

Low	a	a	a	a	a	a	a	a	a
High	a	b	b	b	b	b	b	b	a
Variable	a	a	a	a	ab	ab	b	a	a
Field	a	a	a	a	b	b	b	a	a
Overall	N.S.	**	***	*	*	*	**	N.S.	N.S.

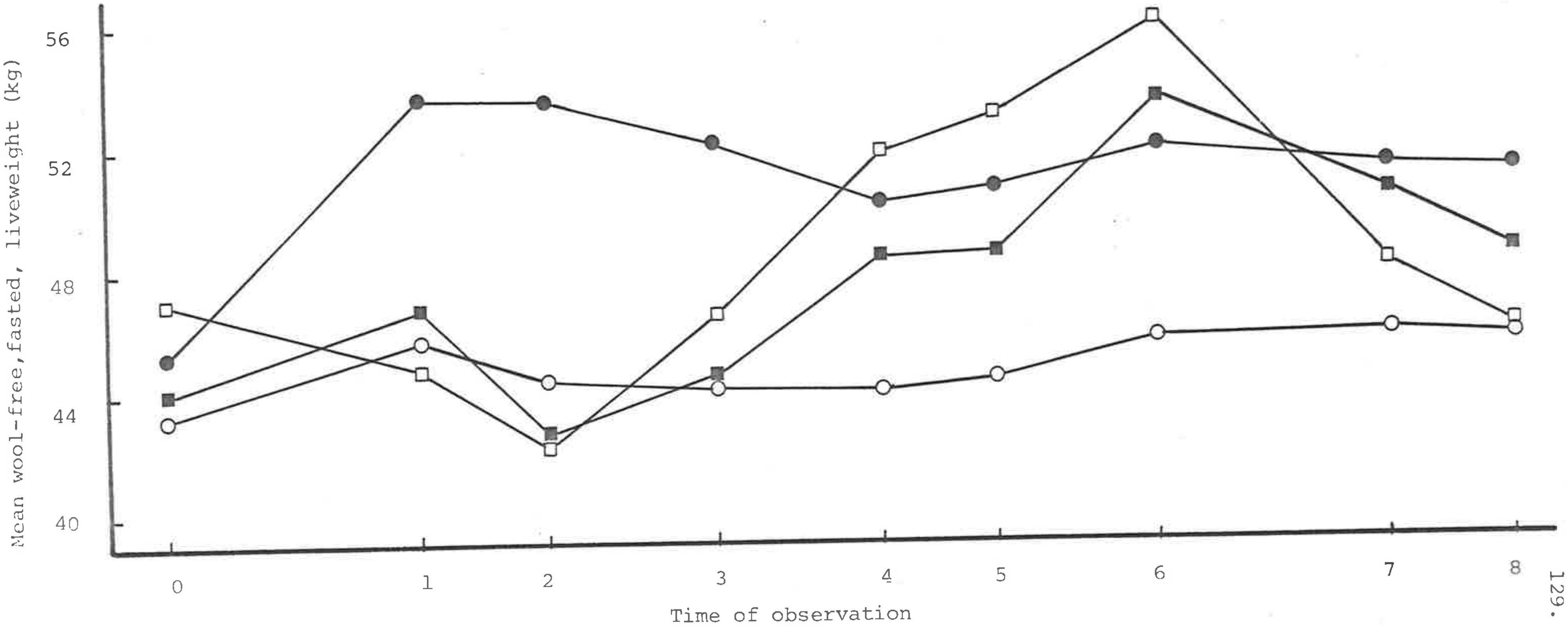


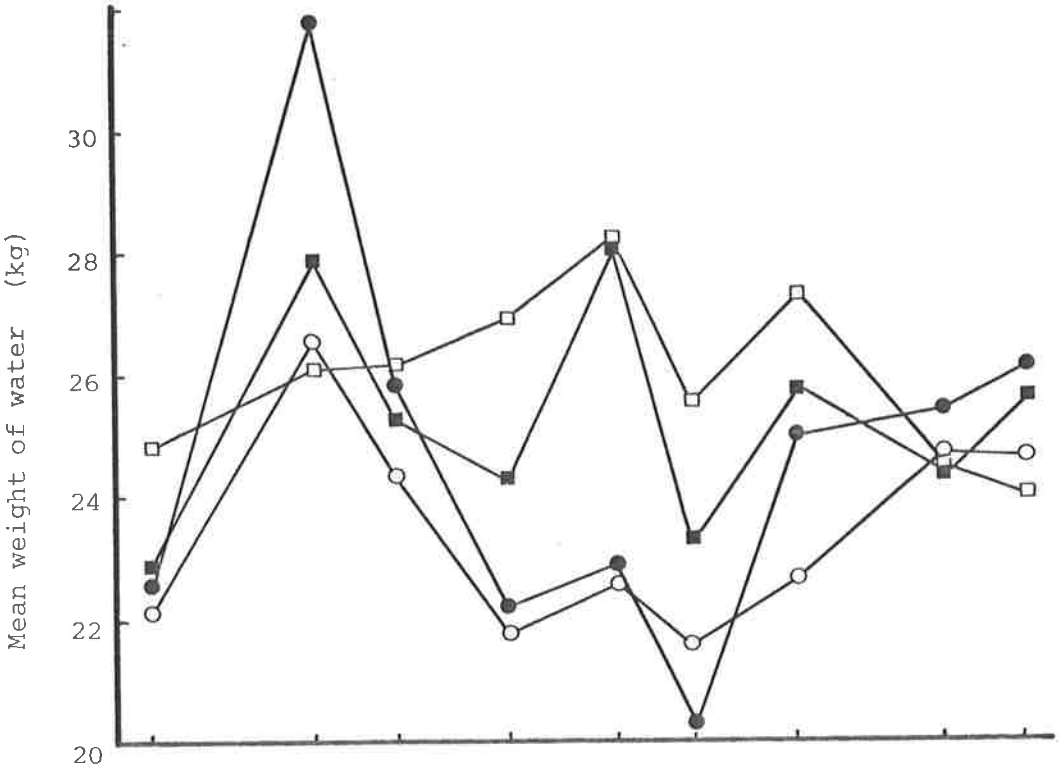
Figure 14. The mean weight of body water (kg) of the Low (○), High (●), Variable (■) and Field (□) group at each Time of observation (Times 0 to 8).

The significance of the difference between individual treatments, and of all treatments, is shown for each Time of observation. Within each Time, treatments having the same letter are not significantly different; treatments with different letters differ at the 5%, or lower, level of significance; and the overall level of significance is indicated by standard notation (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; N.S., not significant).

Figure 15. The mean weight of lean of the Low (○), High (●), Variable (■) and Field (□) group at each Time of observation (Times 0 to 8).

The significance of the difference between individual treatments, and of all treatments, is shown for each Time of observation. Within each Time, treatments having the same letter are not significantly different; treatments with different letters differ at the 5%, or lower, level of significance; and the overall level of significance is indicated by standard notation (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; N.S., not significant).

Low	a	a	a	a	a	ab	a	a	a
High	a	b	a	a	a	a	b	a	a
Variable	a	a	a	b	b	b	bc	a	a
Field	b	a	a	c	b	c	c	a	a
Overall	*	***	N.S.	***	***	***	***	N.S.	N.S.



Low	a	a	a	a	a	ab	a	a	a
High	a	b	a	a	a	a	b	a	a
Variable	a	a	a	b	b	b	bc	a	a
Field	b	a	a	c	b	c	c	a	a
Overall	*	***	N.S.	***	***	***	***	N.S.	N.S.

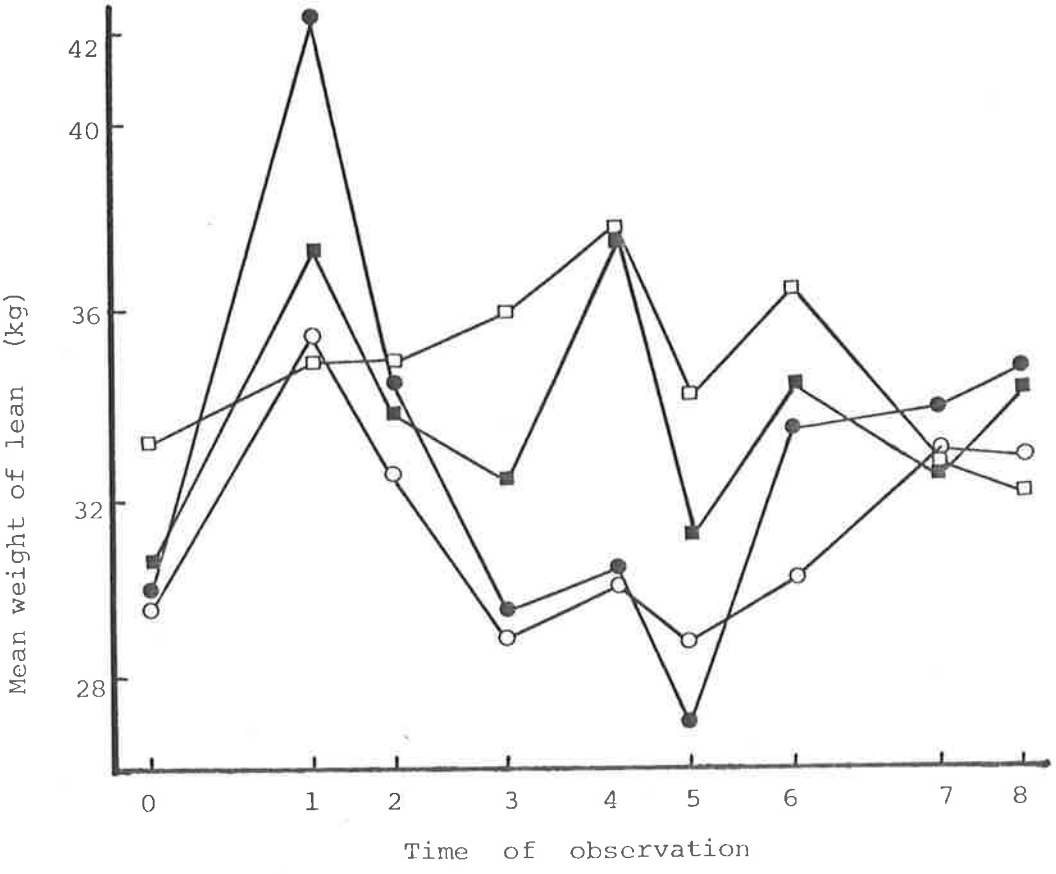


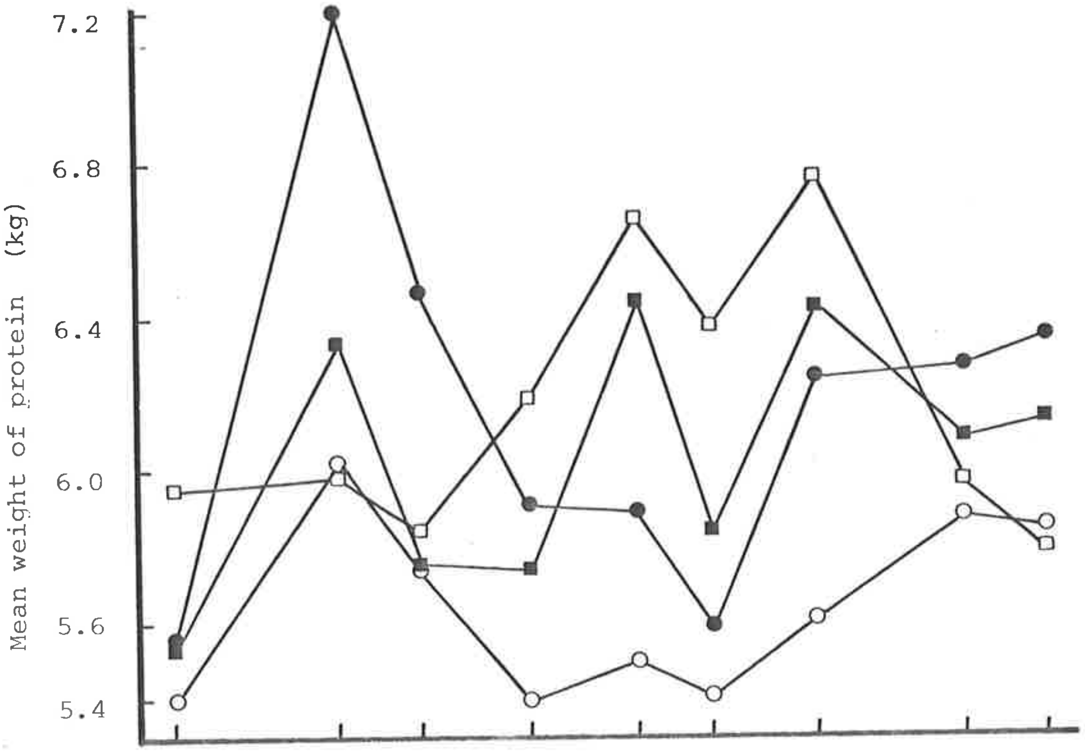
Figure 16. The mean weight of protein (kg) of the Low (○), High (●), Variable (■) and Field (□) group at each Time of observation (Times 0 to 8).

The significance of the difference between individual treatments, and of all treatments is shown for each Time of observation. Within each Time, treatments having the same letter are not significantly different; treatments with different letters differ at the 5%, or lower, level of significance; and the overall level of significance is indicated by standard notation (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; N.S., not significant).

Figure 17. The mean weight of fat (kg) of the Low (○), High (●), Variable (■) and Field (□) group at each Time of observation (Times 0 to 8).

The significance of the difference between individual treatments, and of all treatments, is shown for each Time of observation. Within each Time, treatments having the same letter are not significantly different; treatments with different letters differ at the 5%, or lower, level of significance; and the overall level of significance is indicated by standard notation (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; N.S., not significant).

Low	a	a	a	a	a	a	a	a	a
High	ab	b	a	ab	a	a	b	a	a
Variable	ab	a	a	ab	b	a	bc	a	a
Field	b	a	a	b	b	b	c	a	a
Overall	N.S.	***	N.S.	*	***	**	***	N.S.	N.S.



Low	a	a	**a**	a	a	a	a	a	a
High	a	a	**b**	b	b	b	ab	b	b
Variable	a	a	**ac**	ac	a	a	b	b	ab
Field	a	a	**c**	c	a	a	b	ab	ab
Overall	N.S.	N.S.	***	***	***	**	N.S.	*	N.S.

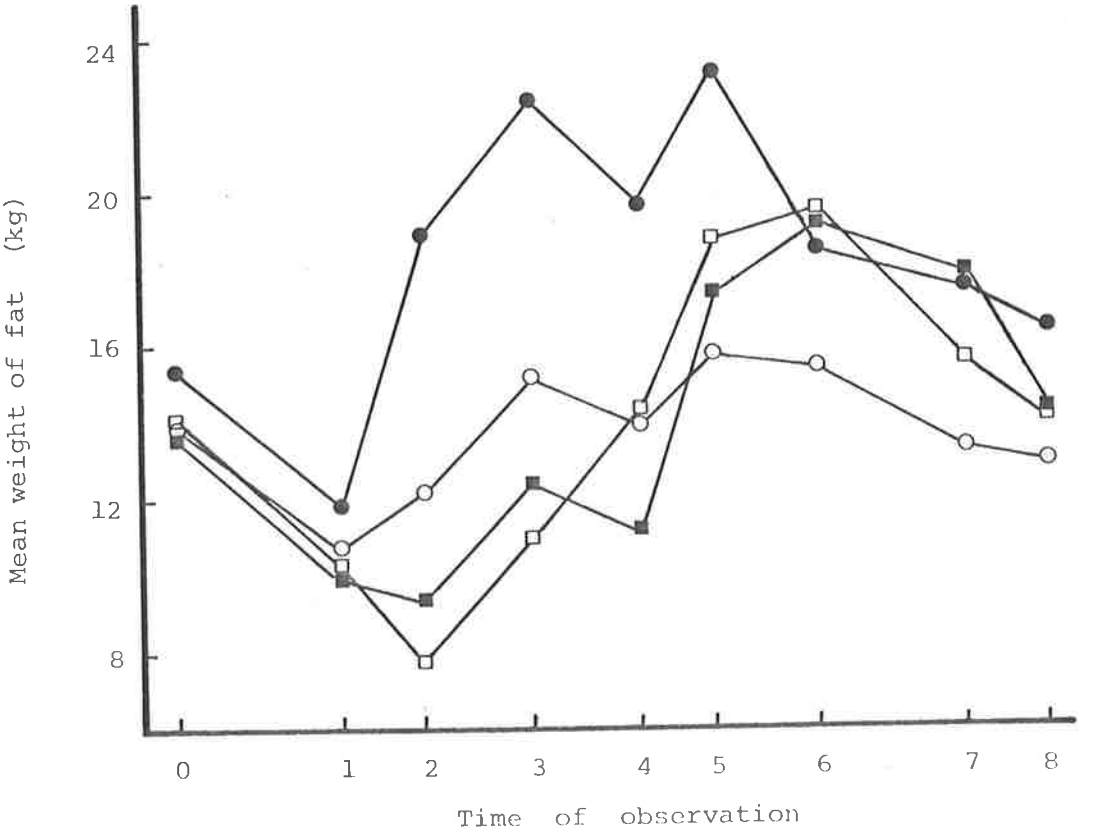


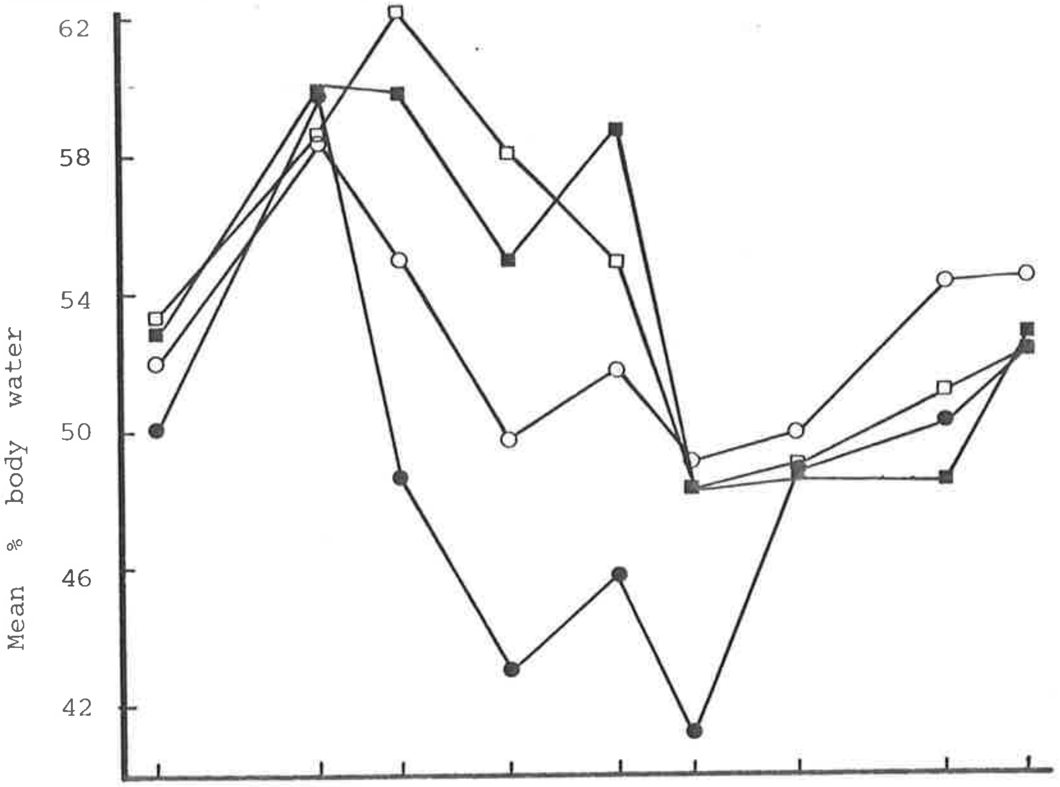
Figure 18. The mean proportion of body water (% of wool-free, fasted liveweight) for the Low (○), High (●), Variable (■) and Field (□) group at each Time of observation (Times 0 to 8).

The significance of the difference between individual treatments, and of all treatments, is shown for each Time of observation. Within each Time, treatments having the same letter are not significantly different; treatments with different letters differ at the 5%, or lower, level of significance; and the overall level of significance is indicated by standard notation (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; N.S., not significant).

Figure 19. The mean proportion of lean (% of wool-free, fasted liveweight) for the Low (○), High (●), Variable (■) and Field (□) group at each Time of observation (Times 0 to 8).

The significance of the difference between individual treatments, and of all treatments, is shown for each Time of observation. Within each Time, treatments having the same letter are not significantly different; treatments with different letters differ at the 5%, or lower, level of significance; and the overall level of significance is indicated by standard notation (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; N.S., not significant).

Low	a	a	a	a	a	a	a	a	a
High	a	a	b	b	b	b	a	b	a
Variable	a	a	c	c	c	a	a	b	a
Field	a	a	c	c	d	a	a	b	a
Overall	N.S.	N.S.	***	***	***	***	N.S.	**	N.S.



Low	a	a	a	a	a	a	a	a	a
High	a	a	b	b	b	b	a	b	a
Variable	a	a	c	c	c	a	a	b	a
Field	a	a	c	c	d	a	a	ab	a
Overall	N.S.	N.S.	***	***	***	***	N.S.	**	N.S.

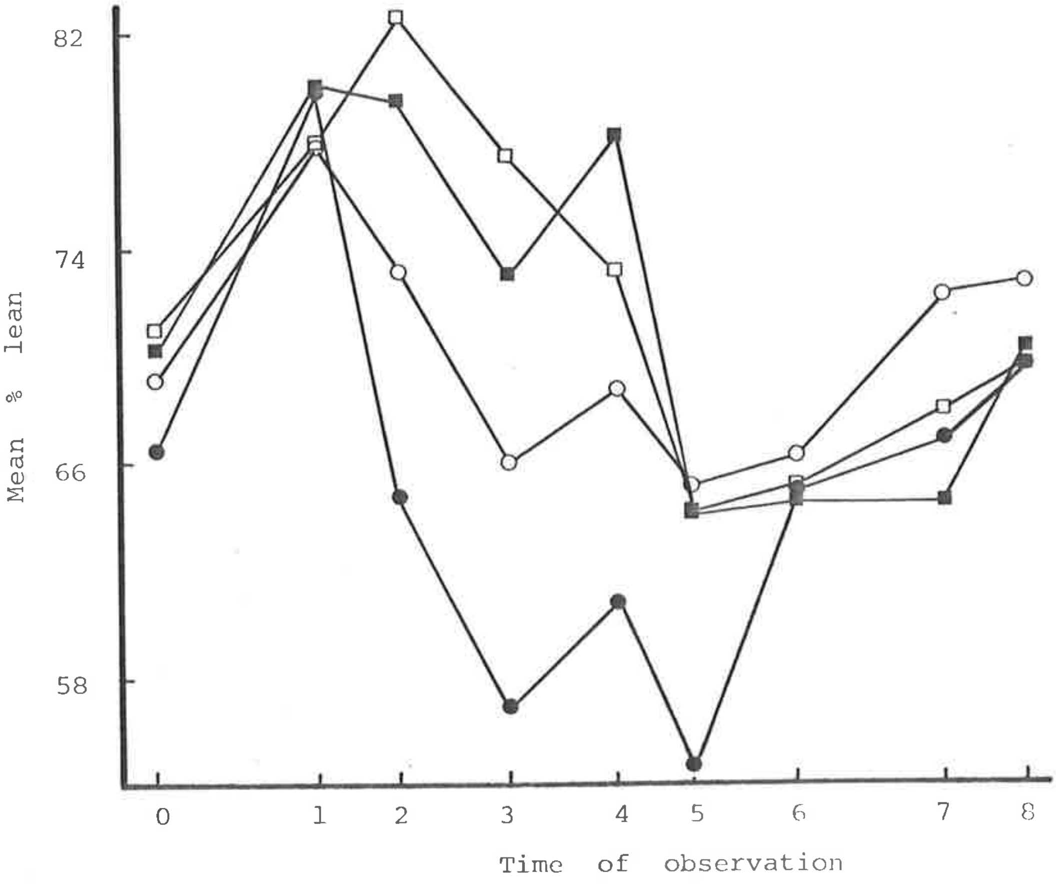


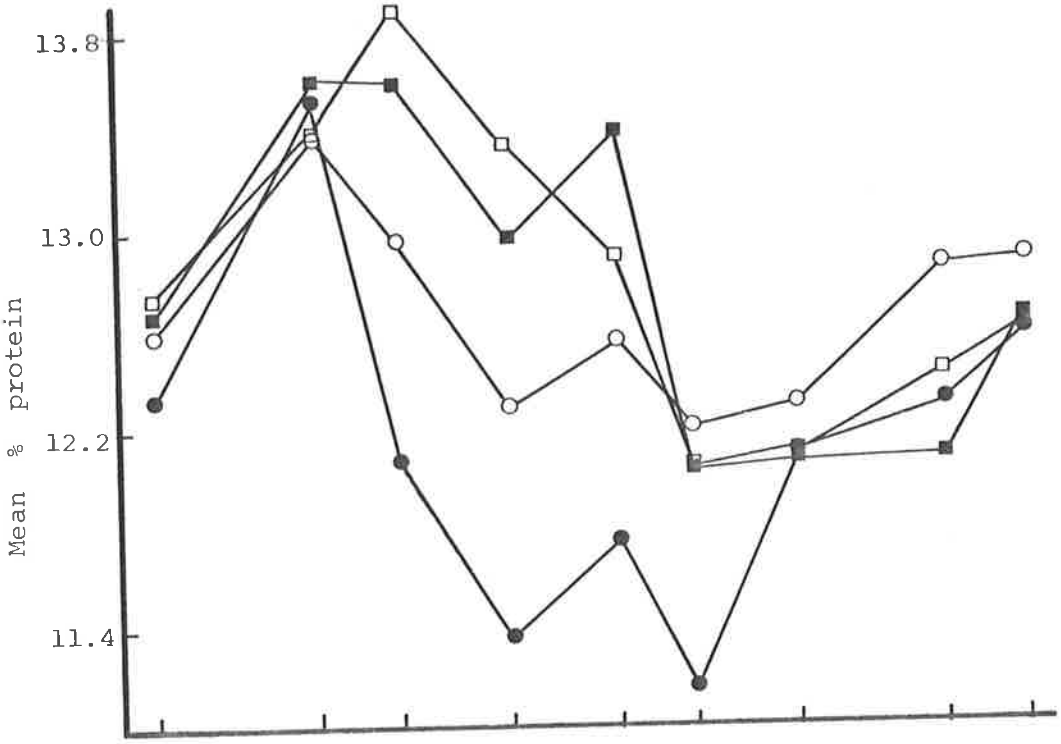
Figure 20. The mean proportion of protein (% of wool-free, fasted, liveweight) for the Low (O), High (●), Variable (■) and Field (□) group at each Time of observation (Times 0 to 8).

The significance of the difference between individual treatments, and of all treatments, is shown for each Time of observation. Within each Time, treatments having the same letter are not significantly different; treatments with different letters differ at the 5%, or lower, level of significance; and the overall level of significance is indicated by standard notation (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; N.S., not significant).

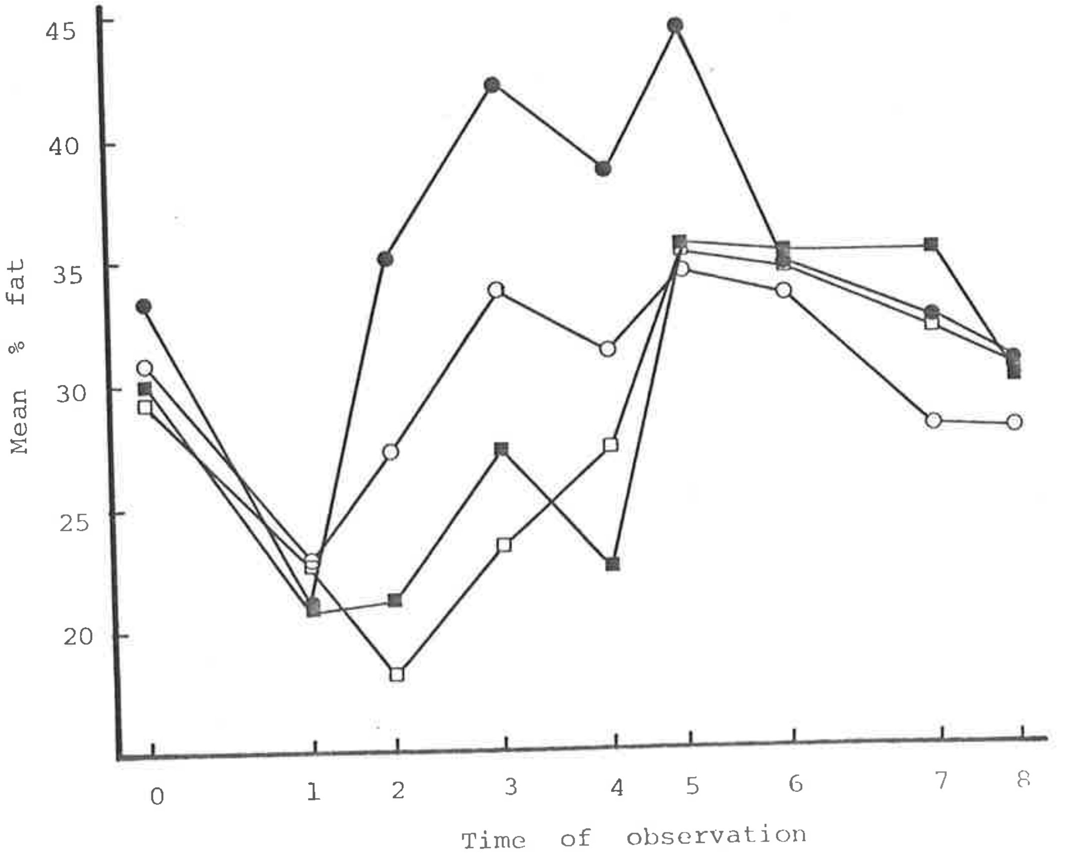
Figure 21. The mean proportion of fat (% of wool-free, fasted liveweight) for the Low (O), High (●), Variable (■) and Field (□) group at each Time of observation (Times 0 to 8).

The significance of the difference between individual treatments, and of all treatments, is shown for each Time of observation. Within each Time, treatments having the same letter are not significantly different; treatments with different letters differ at the 5%, or lower, level of significance; and the overall level of significance is indicated by standard notation (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$); N.S., not significant).

Low	a	a	a	a	a	a	a	a	a
High	a	a	b	b	b	b	a	b	a
Variable	a	a	c	c	c	a	a	b	a
Field	a	a	c	c	a	a	a	b	a
Overall	N.S.	N.S.	***	***	***	**	N.S.	**	N.S.



Low	a	a	a	a	a	a	a	a	a
High	a	a	b	b	b	b	a	b	a
Variable	a	a	c	c	c	a	a	b	a
Field	a	a	c	c	c	a	a	b	a
Overall	N.S.	N.S.	***	***	***	***	N.S.	**	N.S.



and the weight of lean are both dependent upon the same variable, namely, tritiated water space. Thus, while the absolute levels were different, the seasonal patterns of change in these two components were similar.

While the equation for the calculation of weight of protein is dependent on liveweight as well as tritiated water space, the effect of liveweight was not marked. In broad outline the pattern of change in the weight of protein was little different to that of the pattern for water and lean.

The seasonal pattern of change in the weight of fat was markedly different to the pattern for water, lean and protein.

The similarities and differences in the seasonal pattern of the various components, and of liveweight, can be seen for each treatment group by overlaying the relevant data of Figures 14, 15, 16, 17 and 13 respectively. These overlays are depicted for the Low, High, Variable and Field Groups in Appendix Figures 1, 2, 3 and 4 respectively.

When the various components are considered as a percentage of wool-free, fasted liveweight % protein varies in harmony with % water and % lean; as the liveweight variate in the equation for estimating protein cancels out all three variables are directly related to tritiated water space. Overlays of the relevant percentage data shown in Figures 18, 19, 20 and 21, and for liveweight are depicted for the Low, High, Variable and Field groups in Appendix Figures 5, 6, 7 and 8, respectively.

Consideration of Appendix Figures 1 to 8 shows that there are basically only four seasonal patterns for each treatment group, namely

- water (with lean the same and protein similar)
- fat
- % water (with % lean and % protein the same)
- % fat

(d) Assessment of seasonal patterns of change in body components

In both the Low and High group the mean weight of water, lean and protein appeared to undergo a steady cyclic change with the minimum level occurring in late winter/early spring and the maximum in summer. Duncan's multiple range test indicated that in the Low group the values at Times 3 and 5 were lower than at Times 0, 1, 2, 6, 7 and 8 and in the High group the values were less at Times 0, 3, 4 and 5 than at Times 1, 2, 6, 7 and 8. The magnitude of the cyclic change was greater in the High than in the Low group. The results of the Variable group were in fact variable and there was no indication of a cyclic pattern: in general there was a constant level throughout the year although the values were lower at Times 0, 3, 5 and 7 than at Times 1 and 4. The Field group exhibited an annual cyclic pattern with the minimum level occurring in early winter and the maximum in late winter/spring (Times 0, 7 and 8 < Times 3, 4 and 6).

The mean weight of fat changed in an annually cyclic manner for each of the four groups. The Low (Time 1 < Time 3, 5 and 6) and High groups (Times 0, 1, 7 and 8 < Times 3 and 5; Time 1 < Times 0, 7 and 8 < Times 3 and 5) both had minimum amounts in autumn. The Variable (Times 1 and 2 < Time 0 < Times 5, 6 and 7) and Field groups (Times 1, 2 and 3 < Times 0, 4, 7 and 8 < Times 5 and 6) did not appear to reach their minimum level until a little later, in early winter. Each group attained its maximum weight of fat in late spring. The difference between the minimum (during autumn/winter 1972) and maximum values (during spring 1972) was similar for the Field (11.8 kg), High (11.3 kg) and Variable 9.5 kg) groups but less for the Low group (5.0 kg).

On the basis of a percentage of liveweight the amount of water, protein and lean varied in an annually cyclic manner for each group. In the Low (Times 3 and 5 < Times 1, 2, 7 and 8) and High groups (Times 3 and 5 < Times 0, 1, 6, 7 and 8) the phase and magnitude of the cycle was very similar to that stated previously for the absolute amounts, as liveweight was basically constant over the year. Naturally this was not so for the Variable and Field groups where liveweight varied from season to season. While the situation was not particularly clear for the Variable group it appears that both the Variable (Times 5, 6 and 7 < Times 0, 3 and 8 < Times 1, 2 and 4) and Field groups (Times 5 and 6 < Times 0, 4 and 8 < Times 1, 2 and 3) reached a minimum proportion of water in spring and a maximum in late autumn. The magnitude of the seasonal variation was approximately similar for the High, Variable and Field groups but was less for the Low group.

The pattern of seasonal variation in the percentage of fat was inverse to that for the percentage of water, lean and protein: there was a minimum percentage of fat at the same time as there was a maximum percentage of water, and *vice versa*. The relative amplitude between the groups was similar to that for percentage water.

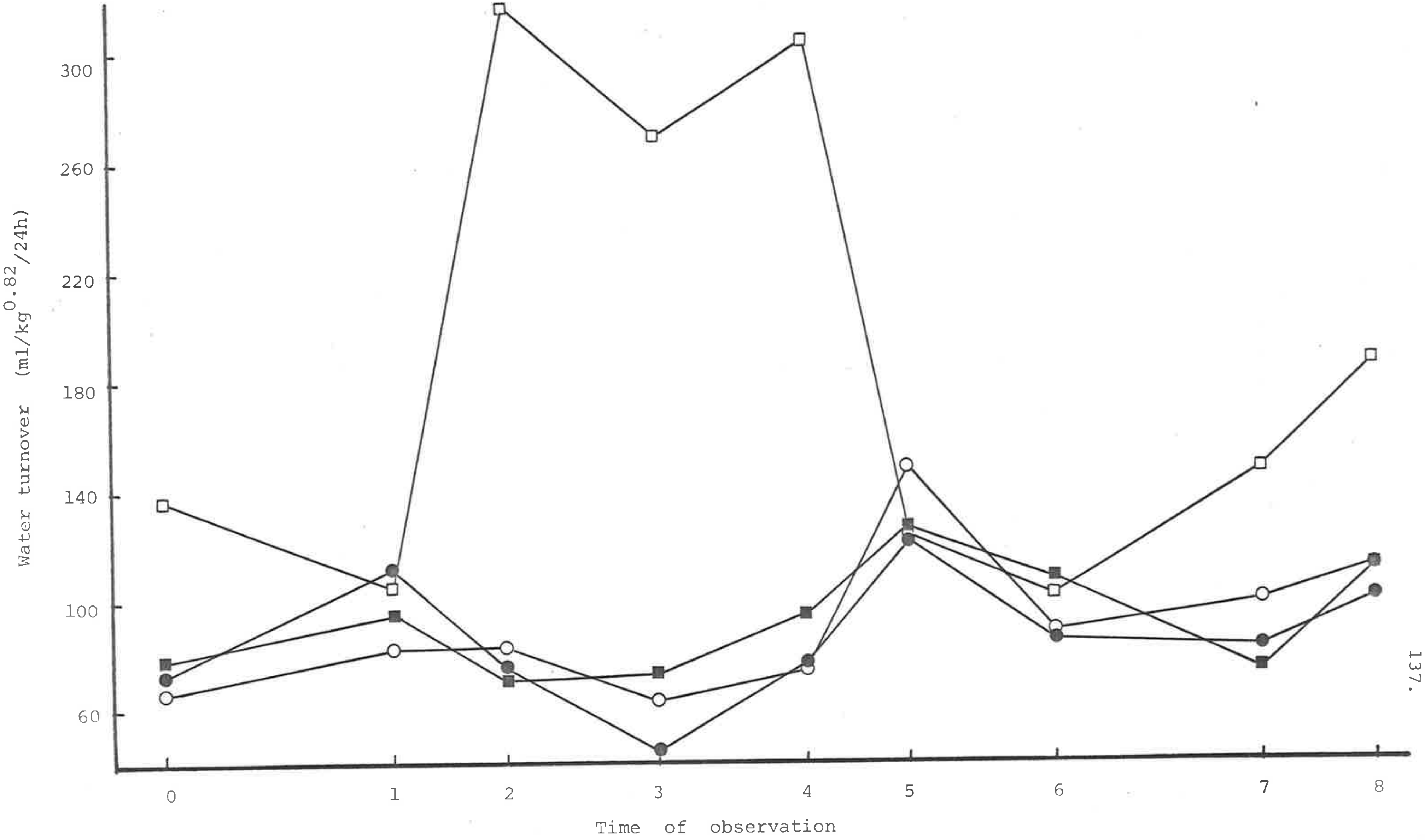
(e) Water turnover

The mean rate of water turnover ($ml/kg^{0.82}/24h$) for each group at each Time of observation is shown in Figure 22. The outstanding

Figure 22. The mean rate of water turnover (ml/kg$^{0.82}$/24 h) for the Low (○), High (●), Variable (■) and Field (□) group at each Time of observation (Times 0 to 8).

The significance of the difference between individual treatments, and of all treatments, is shown for each Time of observation. Within each Time, treatments having the same letter are not significantly different; treatments with different letters differ at the 5%, or lower, level of significance; and the overall level of significance is indicated by standard notation (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$); N.S., not significant).

Low	a	a	a	a	a	a	ab	a	a
High	ab	bd	a	b	ab	b	a	b	a
Variable	b	ac	a	a	b	b	bc	b	a
Field	c	cd	b	c	c	b	c	c	b
Overall	***	*	***	***	***	**	N.S.	***	***



feature was the greatly increased turnover among the Field ewes during the winter and spring of 1972 and during late summer in 1973 (Times 2 and 4 > Time 3 > Time 8 > Times 0, 5 and 7 > Times 1 and 6). By comparison the three pen-fed groups exhibited relatively little seasonal variation in turnover. However, these groups exhibited a significant biannual cycle of change in turnover. The effect was most marked in the High (Times 1, 5 and 8 > Times 0, 2, 4, 6 and 6 > Time 3) and Low (Times 5 and 8 > Times 1, 2 and 6 > Times 0 and 3) groups and less obvious in the Variable group (Time 5 > Times 0, 1, 2, 3 and 7).

(f) Incidence of multiple ovulation and oestrus

Relationships between the various body components and the rate of water turnover, and the incidence of both multiple ovulation and oestrus to day 16 were examined using regression analysis of the group means. This procedure involved several major assumptions that should be borne in mind when assessing the results. Firstly, the body composition data related to only some (71) of the ewes from which the ovulation (203) and oesturs (222) data were obtained. Secondly, as body composition was measured some time after ovulation, estimates of composition at about the average time of ovulation were made from the respective graphs (Figures 14 to 21) about 20 days prior to Times 1, 5 and 8. Linear relationships were assumed between Times of observation. The estimated values are shown in Table 9.

Regression analyses of the data (Table 9) for all treatments on all occasions revealed a significant relationship ($P < 0.05$) between multiple ovulation (y) and protein (x) of $y = 18.26x - 79.54$. The relationship is shown graphically in Figure 23.

Table 9. The incidence of multiple ovulation, and of oestrus to day 16, together with the estimated mean value of water turnover and several body components at ovulation during (a) March 1972, (b) September 1972 and (c) March 1973.

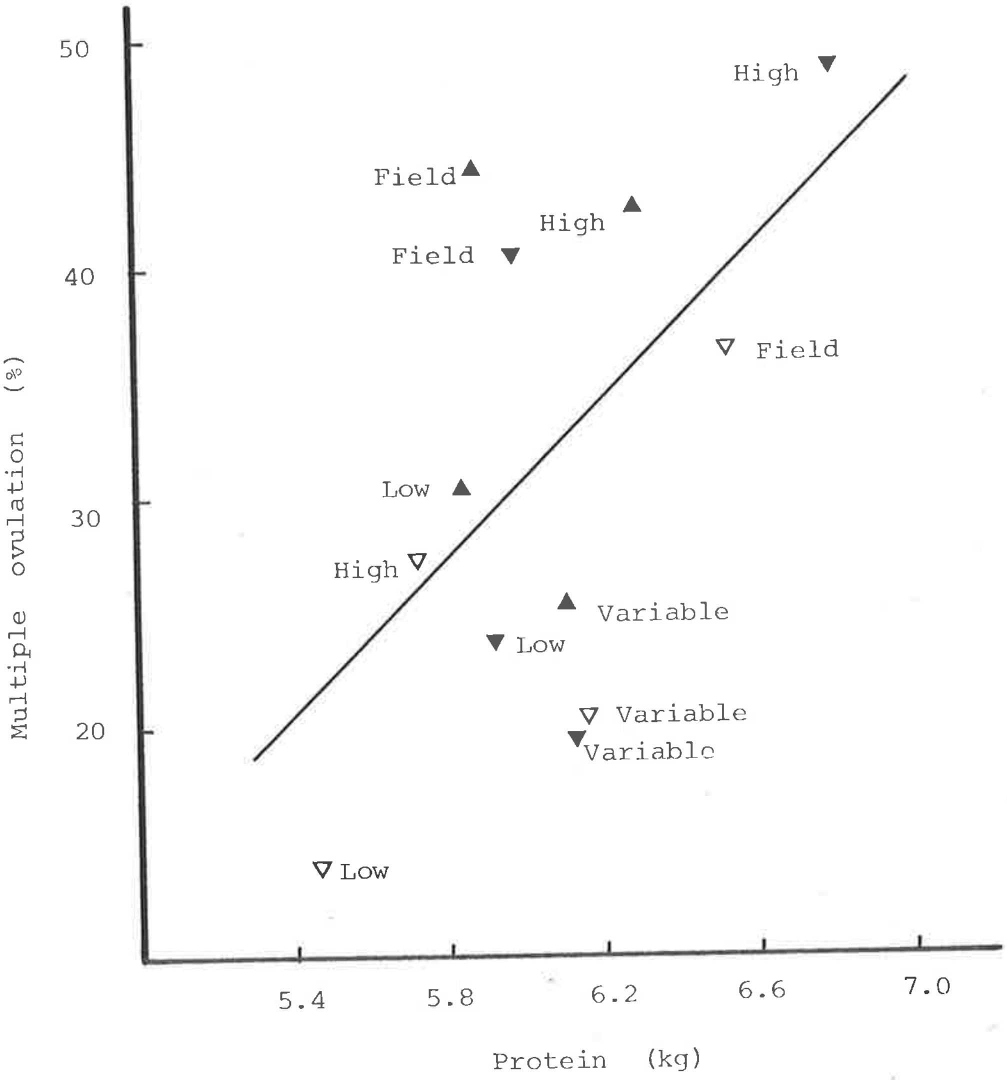
Treatment group	Multiple ovulation (%)	Oestrus to day 16 (%)	Water turnover (ml/kg$^{0.82}$ /24h)	Body component							
				Water (kg)	Lean (kg)	Protein (kg)	Fat (kg)	Water (%)^a	Lean (%)^a	Protein (%)^a	Fat (%)^a
(a) March 1972											
Low	24.0	94.6	78	25.5	34.0	5.92	11.4	56.9	75.6	13.18	24.5
High	49.0	79.6	103	29.6	40.5	6.80	12.6	57.5	76.7	13.00	23.8
Variable	19.6	79.6	91	26.8	35.6	6.13	10.8	58.4	77.7	13.38	22.7
Field	40.7	86.2	113	25.9	34.4	5.98	11.2	57.5	76.3	13.25	24.0
(b) September 1972											
Low	14.0	53.5	110	22.2	29.4	5.45	14.8	50.5	67.0	12.38	32.7
High	27.7	57.4	98	21.7	28.8	5.74	21.1	43.4	57.7	11.47	41.0
Variable	20.5	38.9	110	25.9	34.4	6.16	14.0	53.8	71.7	12.78	30.0
Field	36.7	20.7	220	27.0	36.0	6.53	16.4	51.9	69.0	12.50	31.0
(c) March 1973											
Low	30.8	83.9	106	24.7	32.9	5.85	13.1	54.4	72.2	12.86	27.7
High	42.9	70.4	92	25.8	34.3	6.29	16.8	51.4	68.2	12.44	31.0
Variable	25.5	75.9	94	20.1	33.4	6.11	16.0	51.0	67.5	12.37	32.2
Field	44.4	82.8	168	24.3	32.3	5.88	14.8	51.8	68.8	12.52	31.0

a % of wool-free, fasted liveweight.

Figure 23. Relationship between the incidence of multiple ovulation (%), and mean weight of protein (kg), for each treatment group during March 1972 (▼), September 1972 (▽) and March 1973 (▲).

The linear regression line shown relates to the whole of the data depicted (n=12).

Regression $y = 18.26x - 79.54$ ($P < 0.05$).


Multiple ovulation (%)
50
40
30
20
Protein (kg)
5.4
5.8
6.2
6.6
7.0
High
Field
High
Field
Field
Low
High
Variable
Low
Variable
Variable
Low

There was also a significant negative relationship between the incidence of oestrus to day 16 and water turnover. However, the regression appears to have been fortuitous and resulted from a marked effect of season on both the occurrence of oestrus and the rate of water turnover of the Field ewes in September. Also, such a relationship does not seem to be sensible physiology. It appears reasonable to completely discount the relationship.

2. DISCUSSION

The treatments imposed influenced the season of the year during which the maximum and minimum levels of the various body components occurred. The effect was greater for water (lean and protein) than for fat content. The maximum level of mean water content was recorded for both the Low and High groups during summer and for the Field group during late winter/spring. Minimum levels were recorded during late winter/early spring and early winter, respectively. The Variable group did not exhibit an obvious cyclic pattern. In contrast to the markedly different phase of the seasonal change in water content the patterns of seasonal change in fat content were only slightly out of phase. The maximum content occurred in each group during late spring while the minimum for the High and Low groups occurred during autumn and for the Variable and Field groups during early winter. The differences in phase of the cyclic variation in the proportion of water (% water) in the body was not as marked as for water. Maximum proportions occurred in the High and Low groups during summer and in the Variable and Field groups during late winter/early spring and spring, respectively. The maximum and minimum proportions of fat occurred during the seasons of minimum and maximum proportion of water, respectively (i.e. an inverse relationship).

In view of the differences in phase, the level and dynamic state of the various body components obviously varied between treatments, at the times oestrus and ovulation were measured. In March 1972 the High and Low groups had reached their maximum amount of water (lean and protein) and their minimum amount of fat. In contrast the Field group was still gaining water and losing fat. In September 1972 the High and Low groups had reached their minimum amount of water and almost reached their maximum amount of fat. In contrast the Field group had reached its maximum amount of water but, similarly to the High and Low groups, was approaching its maximum amount of fat. In March 1973 the Low and Field groups appear to have been in a similar situation to that in March 1972. The High group might not quite have reached its maximum water and minimum fat levels. With one exception, expressing the component as a proportion of wool-free, fasted, liveweight did not alter the status compared with that of the absolute amount of the component. The exception was the Field group in September 1972 when the proportion of water had fallen rapidly almost to a minimum level whereas in absolute terms there was a maximum amount of water.

The very large increase in the mean rate of water turnover among the Field ewes during winter 1972 and the smaller increase during summer 1973 were obvious, and expected, responses to the green feed available during those periods, the latter occurring following considerable summer rainfall. There is not an equally obvious explanation for the smaller, but significant, biannual fluctuation in the rate of turnover among the pen-fed groups. However, the daily temperatures experienced during each seven-day measurement period might have been important. At Time 0 the temperature was mild for that time of the year (average maximum 25.5°C, minimum 13.6°C) while at Time 1 three of the seven days were unusually hot (daily maxima 33.7, 36.2 and 32.6°C). The temperatures at Time 5 were lower than expected for October (average maximum 17.6°C, minimum 7.5°C). These abnormalities might have lowered the turnover at Times 0 and 5 and raised it at Time 1. The turnover at Time 0 could also have been depressed by the generally unpalatable nature of the feed offered at that time. Clarke and Quinn (1949) found that water intake decreased as the intake of dry feed decreased. If these effects did occur then the seasonal variation in turnover reverts, with the exception of an increase during October, to one with an annual cycle basically in phase with the annual temperature cycle.

While the association between ovulatory performance and the estimated mean weight of protein was rather uncertain it should be noted that it was markedly better than the association of any of the other components, or component proportions, with ovulation. This is an interesting point for, although work with high protein lupin supplementation suggests a rapid response in ovulation under certain circumstances (low quality feed, mature age ewes, and (?) ewes in poor condition), there has been no report specifically relating nutritionally induced differences in body protein to ovulation rate. This association is consistent with the hypothesis that ovulatory activity is related to the 'net nutritional status' of ewes (Lindsay, 1976). All other things being equal, those ewes with greater amounts of body protein could have a greater endogenous contribution of nutrients to their nutritional status. Further substantiating information from detailed studies is necessary before a relationship between body protein and ovulation could be regarded as reasonably certain.

3. SUMMARY

(1) Apart from the water content of the Variable ewes (which did not fluctuate) the average of each body component (water, lean, protein) fluctuated on an annual basis for each treatment. The season during which the maximum and minimum values occurred varied between components and between treatments.

(2) There was considerable variation between treatments in the level and dynamic state of the various components at each time oestrus and ovulation was measured. In March 1972 the High and Low groups had a maximum amount of water and a minimum amount of fat while the Field group was gaining water and losing fat. There was a similar situation in March 1973 except that the High group had not quite reached its maximum water, or its minimum fat, level. In September 1972 the High and Low groups had a minimum amount of water and had almost reached their maximum amount of fat. The Field group also had a maximum amount of fat but had reached its maximum amount of water.

The level and state of the components on a relative basis was similar to that of the absolute data except for the field group in September when the proportion of water had fallen rapidly to a minimum.

(3) The mean rate of water turnover of the Field ewes increased from about 120 ml/kg$^{0.82}$/24h when they were grazing dry pasture to about 300 and 180 ml/kg$^{0.82}$/24h when grazing green pasture during winter 1972 and autumn 1973, respectively.

There was a small significant biannual fluctuation in the rate of turnover among each of the pen-fed groups. Consideration of temperature and nutritional factors accounts for the biannual nature of the variation and reduces it to an annual cycle in phase with the annual temperature cycle, although an isolated increase in turnover during October remains unexplained by this hypothesis.

(4) There was an uncertain association between the estimated mean weight of body protein at ovulation and the incidence of multiple ovulation.

WITHIN-FLOCK RELATIONSHIPS

(a) LIVEWEIGHT, BODY SIZE, BODY CONDITION

D. WITHIN-FLOCK RELATIONSHIPS WITH OVULATION RATE (a) LIVEWEIGHT, BODY SIZE AND BODY CONDITION

Within-flock relationships between ovulation rate (OR) and wool-free, fasted liveweight at ovulation (LW), body size (BS) and body condition index at ovulation (BC) were examined using information from the 203 ewes with complete sets of ovulation data mentioned previously. The effect of treatment was removed by adjusting the individual values of OR, LW, BS and BC for differences in treatment means (adjusted data).

The data were examined in two ways. Firstly, the adjusted data were ranked, in turn, in descending order of the adjusted value of the variable being examined (LW, BS, BC) and then blocked (grouped) into eight descending groups (octiles). The sets of mean values for the octiles are shown in Table 10. These condensed data were then examined by regression analysis. Secondly, the individual data, adjusted but not condensed, were examined by partial correlation analysis.

The body size of each ewe was measured both at the beginning and the end of the experiment. As shown in Appendix Table 8 the mean size of the Low and High ewes varied significantly over the course of the experiment. Therefore the average of the two measurements of each ewe was considered the most appropriate estimate of its body size to use throughout the experiment.

1. RESULTS

(a) Data grouped into octiles (grouped data)

(i) Wool-free, fasted, liveweight

The mean value of LW and OR for each octile formed after the data were ranked on LW (adjusted for differences in treatment

Table 10. Ovulation rate (OR), liveweight (LW), body size (BS) and body condition (BC) of each octile formed after ranking on either adjusted liveweight, adjusted body size or adjusted body condition.

Octile	Adjusted liveweight				Adjusted body size				Adjusted body condition			
	OR	LW	BS	BC	OR	LW	BS	BC	OR	LW	BS	BC
(a) *March 1972*												
1	1.40	56.04	40.18	1.398	1.39	53.82	42.10	1.278	1.37	52.79	36.31	1.452
2	1.51	52.66	39.23	1.346	1.43	51.51	39.44	1.309	1.51	50.72	36.49	1.391
3	1.24	49.95	37.50	1.336	1.29	49.07	37.66	1.302	1.50	48.37	36.08	1.341
4	1.38	47.76	36.78	1.305	1.26	46.90	36.70	1.277	1.24	48.82	37.40	1.305
5	1.32	45.87	35.52	1.293	1.27	45.89	35.67	1.284	1.10	46.92	36.96	1.270
6	1.20	43.70	35.24	1.243	1.44	44.66	34.67	1.288	1.36	45.54	36.89	1.236
7	1.35	41.14	33.65	1.228	1.31	42.21	33.48	1.262	1.31	41.91	35.25	1.188
8	1.08	35.19	32.44	1.092	1.10	38.31	30.80	1.244	1.11	37.22	35.12	1.058
(b) *September 1972*												
1	1.24	59.56	40.82	1.462	1.17	56.82	42.10	1.350	1.37	56.02	36.60	1.528
2	1.25	54.00	38.56	1.408	1.19	52.62	39.44	1.333	1.13	52.28	36.35	1.438
3	1.35	50.75	37.36	1.362	1.14	48.74	37.66	1.293	1.30	49.96	36.03	1.385
4	1.15	49.02	36.69	1.342	1.17	48.32	36.70	1.316	1.38	48.79	36.54	1.334
5	1.18	47.02	35.61	1.321	1.30	46.60	35.67	1.305	1.15	48.44	37.06	1.307
6	0.88	44.89	35.05	1.283	1.04	46.01	34.67	1.328	1.04	46.23	36.28	1.262
7	1.24	41.74	33.59	1.250	1.20	43.90	33.48	1.311	1.04	44.42	36.94	1.200
8	1.04	35.71	32.88	1.092	1.13	39.80	30.80	1.288	0.93	36.54	34.36	1.067
(c) *March 1973*												
1	1.49	60.16	40.60	1.485	1.38	56.70	42.10	1.346	1.37	55.66	35.87	1.549
2	1.37	54.82	38.96	1.413	1.43	53.83	39.44	1.363	1.58	55.08	38.10	1.447
3	1.39	51.73	36.98	1.401	1.52	49.10	37.66	1.302	1.34	50.60	36.44	1.387
4	1.42	49.29	38.87	1.340	1.25	49.41	36.70	1.342	1.36	48.80	36.17	1.349
5	1.40	47.13	35.42	1.333	1.37	45.62	35.67	1.276	1.52	48.68	37.06	1.312
6	1.36	44.41	34.59	1.285	1.35	46.52	34.67	1.339	1.20	46.47	36.58	1.269
7	1.36	41.71	34.82	1.202	1.27	43.87	33.48	1.331	1.33	42.24	35.07	1.200
8	1.06	35.44	32.31	1.107	1.26	39.81	30.80	1.291	1.13	37.17	35.24	1.056

means) is shown towards the left hand side of Table 10. Each time of observation (March 1972, September 1972, March 1973) was examined separately.

There was a significant linear regression between OR (y) and LW (x) in both March 1972 and March 1973 ($P < 0.05$). The equations were $y = 0.015x + 0.611$ and $y = 0.013x + 0.712$, respectively. These two equations had equal intercept and equal slope. Both sets of data were therefore pooled and analysed as 16 pairs of values to give the equation $y = 0.014x + 0.659$ ($P < 0.001$). The equation for September 1972 of $y = 0.0098x + 0.698$ was not significant ($P = 0.21$). The slope, but not the intercept, was similar to that for March 1972, March 1973 and March 1972 and 1973 combined. The significant relationships for March 1972, March 1973, and March 1972 and 1973 are shown in Figure 24. The non-significant regression for September 1972 is also shown.

(ii) Body size

The mean value of BS and OR for each octile formed after the data were ranked on BS (adjusted for differences in treatment means) is shown in the middle of Table 10.

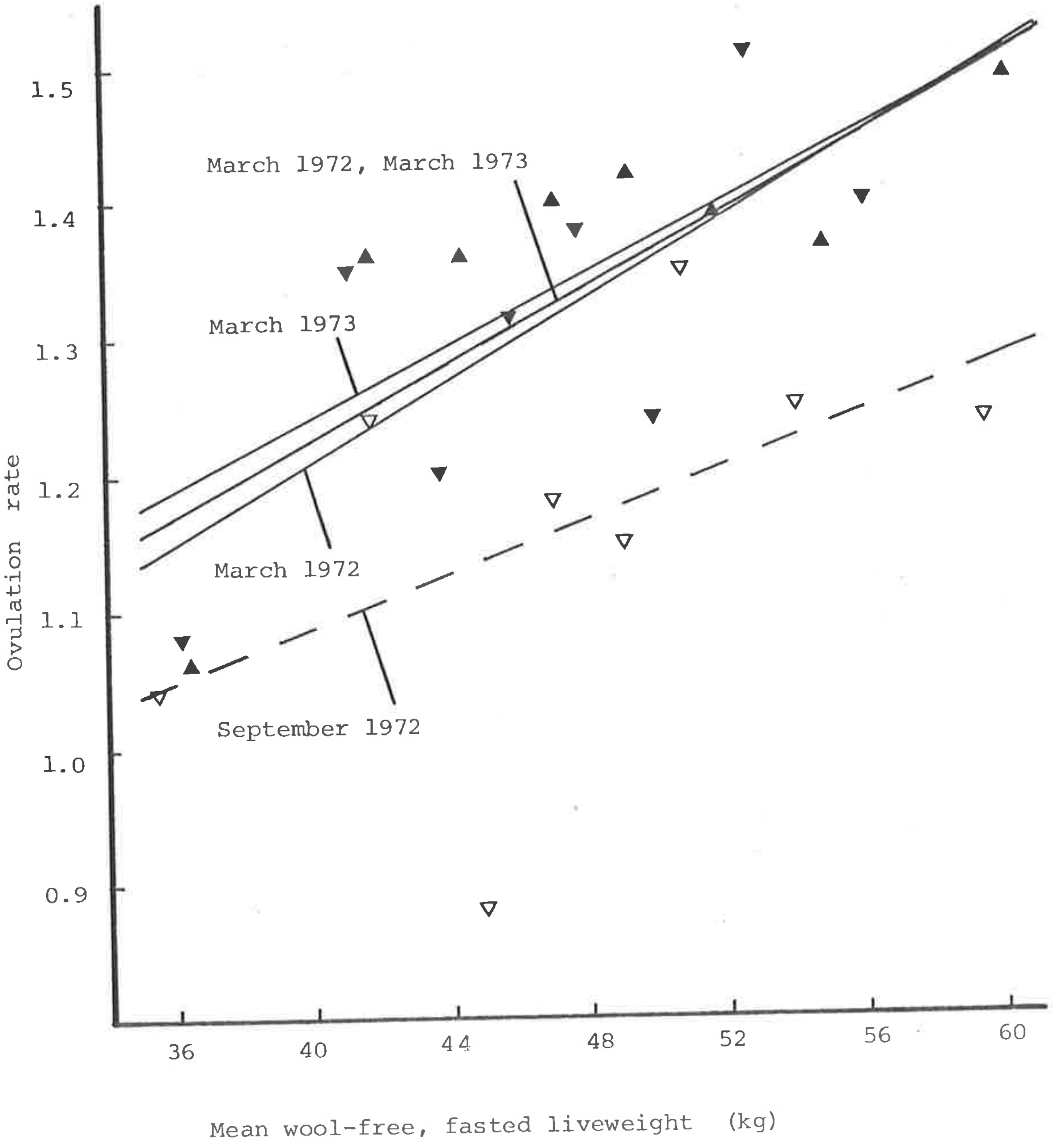
There was not a significant linear regression between OR (y) and BS (x) at any individual time of observation, but the relationships in March 1972 and March 1973 were more nearly significant ($P = 0.086$ and 0.134) than that in September 1972 ($P = 0.66$). Examination of the two sets of March data showed that they had statistically similar slope and intercept. The two sets were therefore pooled and analysed as 16 pairs of values: this revealed a significant relationship ($P < 0.05$) of $y = 0.018x + 0.681$.

Figure 24. The relationship between ovulation rate and mean wool-free, fasted, liveweight (kg) for each liveweight octile in March 1972 (▼), September 1972 (▽) and March 1973 (▲).

Linear regression lines are shown for each set of octiles (n=8) and for the pooled data for March 1972 and March 1973 (n=16).

Regressions

March 1972	$y = 0.015x + 0.611$ ($P < 0.05$).
September 1972	$y = 0.0098x + 0.698$ (N.S.).
March 1973	$y = 0.013x + 0.712$ ($P < 0.05$).
March 1972, March 1973	$y = 0.014x + 0.659$ ($P < 0.001$).


Ovulation rate
1.5
1.4
1.3
1.2
1.1
1.0
0.9
March 1972, March 1973
March 1973
March 1972
September 1972
36
40
44
48
52
56
60
Mean wool-free, fasted liveweight (kg)

When the accumulated ovulatory performance of each ewe was considered over the three times of observation, and at the two March observations, there were significant relationships ($P < 0.05$) of $y = 0.040x + 2.390$, and $y = 0.036x + 1.362$, respectively. The three significant relationships between OR and BS are depicted in Figures 25, 26 and 27. The effect of season (March, September) could not be examined statistically as the regression relationship in September was very poor ($P = 0.66$).

(iii) Body condition

The mean value of BC and OR for each octile formed after the data were ranked on BC (adjusted for differences in treatment means) is shown on the right hand side of Table 10.

There was a significant linear regression relationship between OR (y) and BC (x) in September 1972 of $y = 0.928x - 0.054$ ($P < 0.05$). The regression equations of $y = 0.823x + 0.257$, and $y = 0.622x + 0.533$ for March 1972 and March 1973, respectively, were not significant at the 5% level ($P = 0.082$ and 0.093). However, as these two regressions had statistically similar slope and intercept the two sets of data were pooled and analysed as 16 pairs of values. This revealed the significant regression of $y = 0.710x + 0.409$ ($P < 0.01$). The equation for September 1972 had statistically equal slope with those for March 1972, March 1973 and March 1972 and 1973 combined but in each instance the intercept was not equal. The significant relationships for the pooled data of March 1972 and 1973 and for September 1972 are shown in Figure 28. The two non-significant relations for March 1972 and March 1973 are also shown.

(iv) Inter-relation of LW, BS and BC

Regression analyses of the condensed data were conducted not only between ovulation rate and the factor (LW, BS, BC) on

Figure 25. The relationship between ovulation rate and mean body size ($cm^3 \times 10^{-3}$) for each body size octile in March 1972 (▼) and March 1973 (▲).

The linear regression line shown relates to the whole of the data depicted (n=16).

Regression $y = 0.018x + 0.681$ ($P < 0.05$).

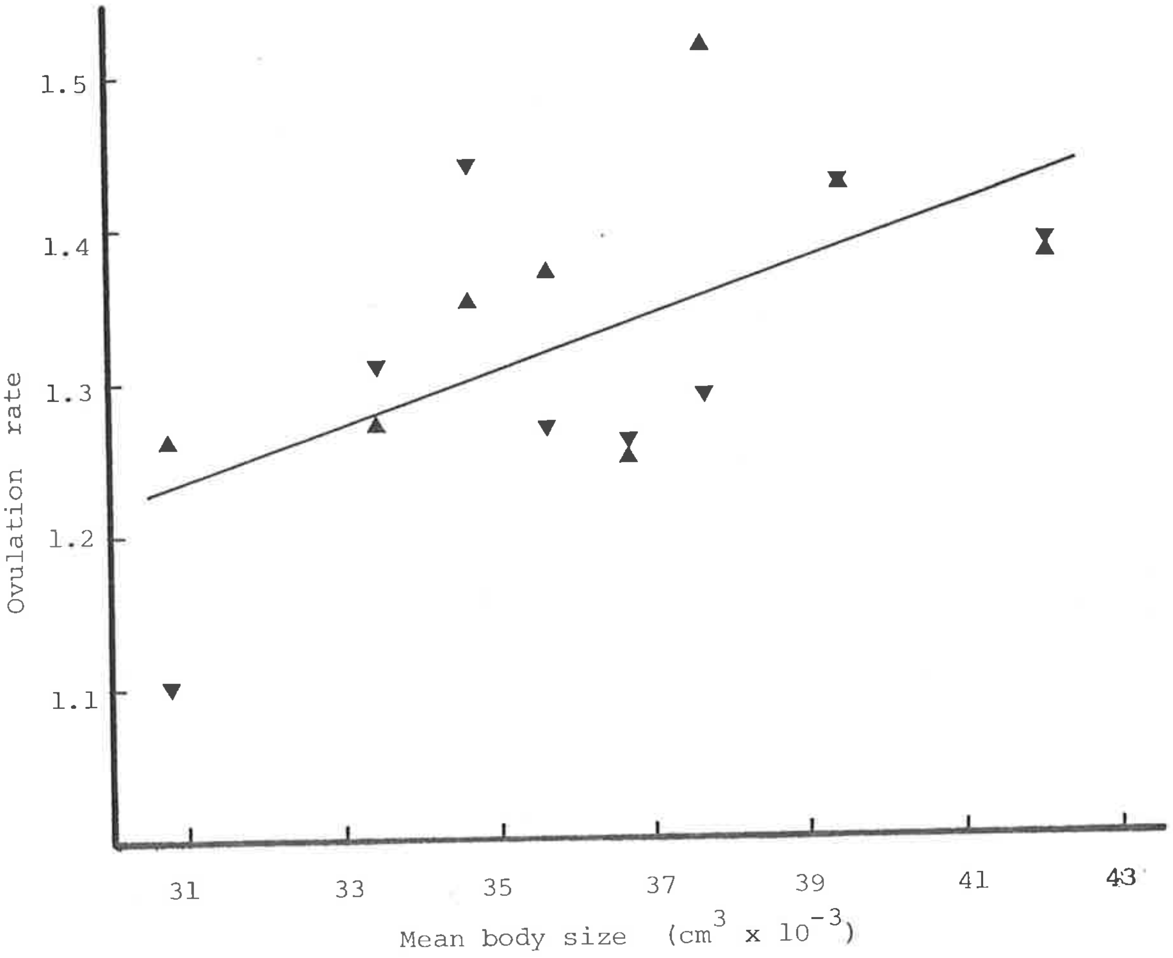

1.5
1.4
1.3
1.2
1.1
Ovulation rate
31
33
35
37
39
41
43
Mean body size (cm3 x 10-3)

Figure 26. The relationship between ovulation rate (accumulated over observations during March 1972, September 1972 and March 1973), and mean body size ($cm^3 \times 10^{-3}$) for each body size octile.

Regression $y = 0.040x + 2.390$ ($P < 0.05$).

Figure 27. The relationship between ovulation rate (accumulated over observations during March 1972 and March 1973) and mean body size ($cm^3 \times 10^{-3}$) for each body size octile.

Regression $y = 0.036x + 1.362$ ($P < 0.05$).

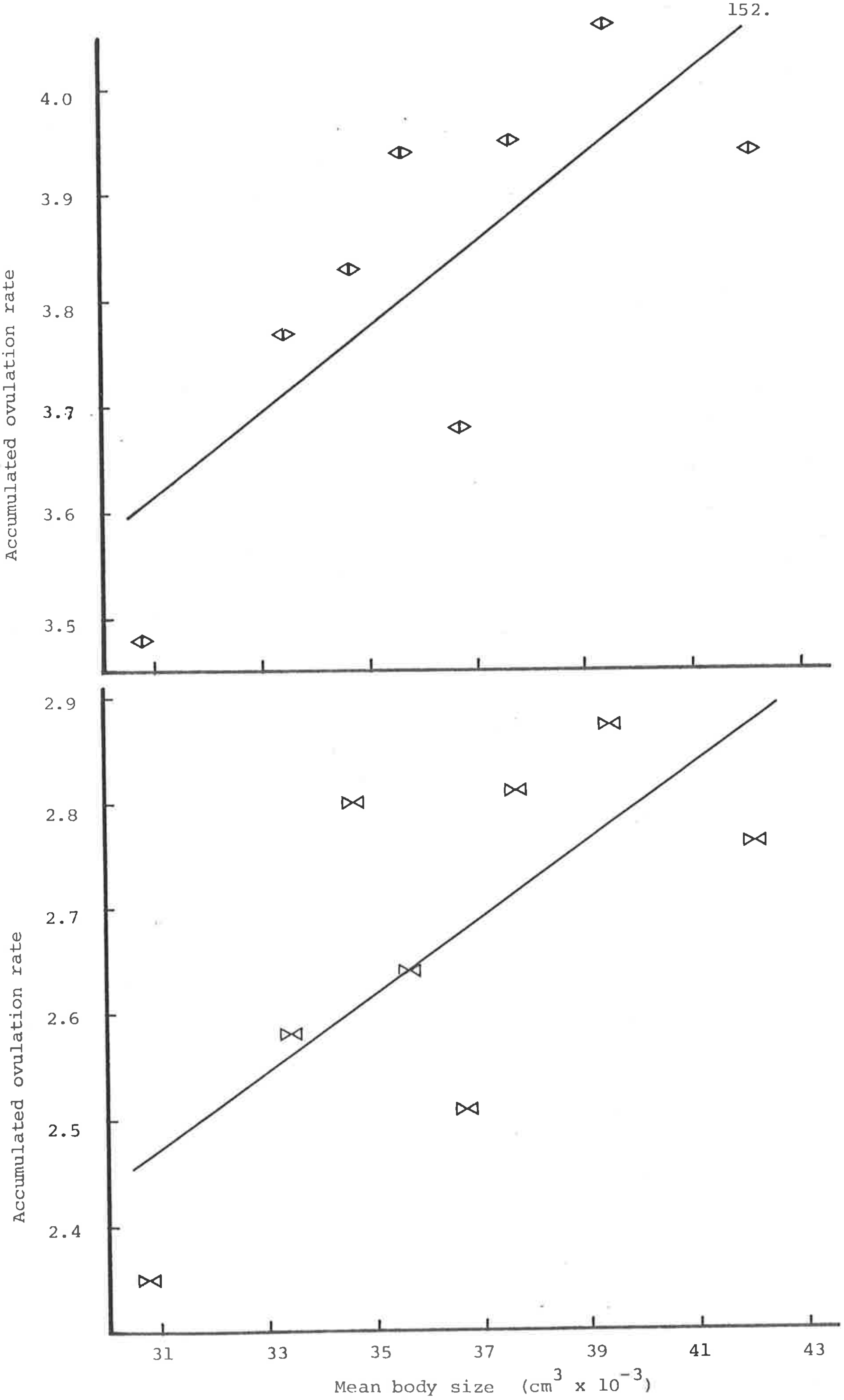
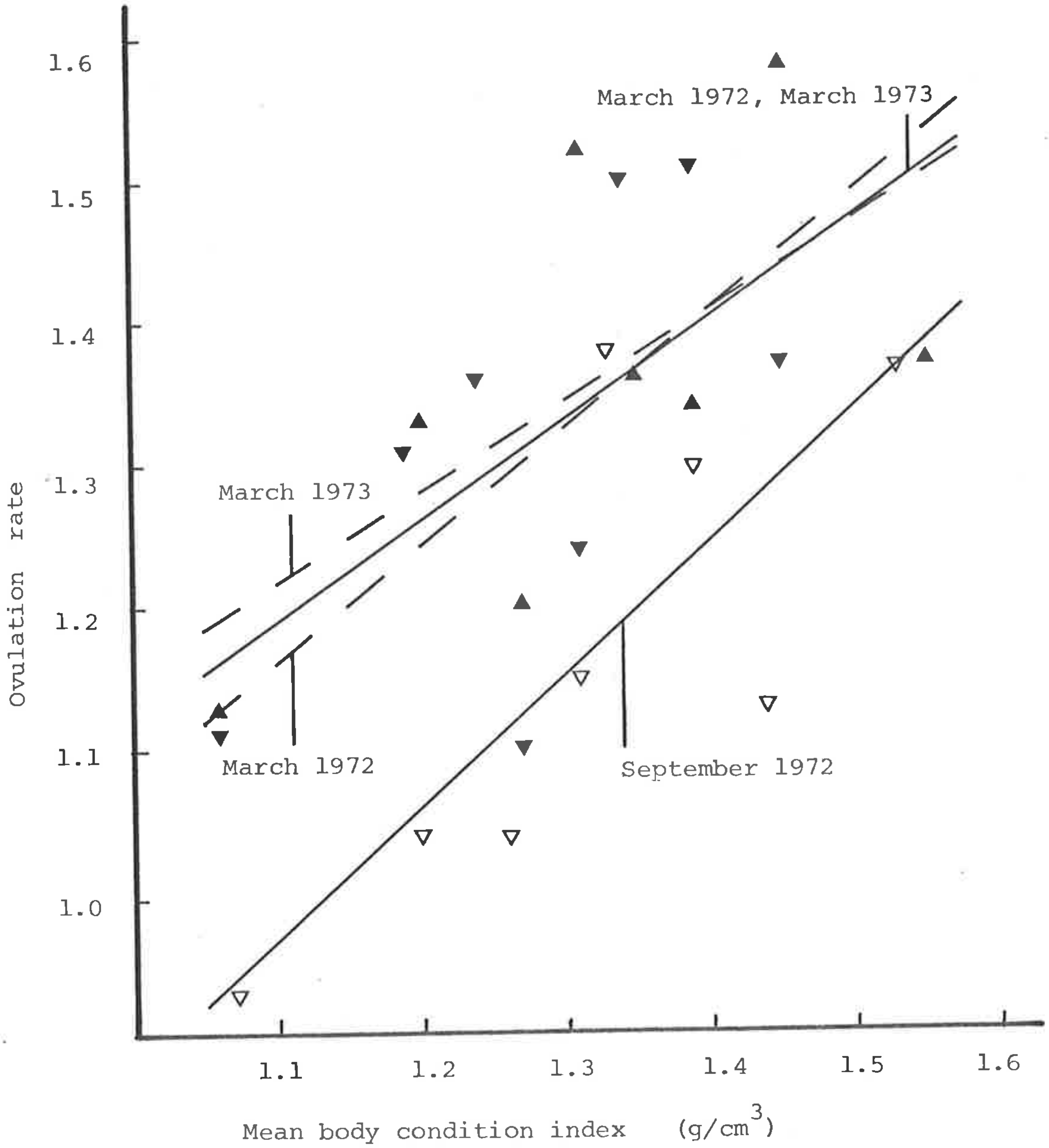

Accumulated ovulation rate
4.0
3.9
3.8
3.7
3.6
3.5
Accumulated ovulation rate
2.9
2.8
2.7
2.6
2.5
2.4
31
33
35
37
39
41
43
Mean body size (cm^3 x 10^{-3})

Figure 28. The relationship between ovulation rate and mean body condition index (g/cm^3) for each body condition octile in March 1972 (▼), September 1972 (▽) and March 1973 (▲).

Linear regression lines are shown for each set of octiles (n=8) and for the pooled data for March 1972 and March 1973 (n=16).

Regressions

March 1972	$y = 0.823x + 0.257$ (N.S.)
September 1972	$y = 0.928x - 0.054$ ($P < 0.05$)
March 1973	$y = 0.622x + 0.533$ (N.S.)
March 1972, March 1973	$y = 0.710x + 0.409$ ($P < 0.01$)


March 1972, March 1973
March 1973
March 1972
September 1972
Ovulation rate
1.6
1.5
1.4
1.3
1.2
1.1
1.0
1.1
1.2
1.3
1.4
1.5
1.6
Mean body condition index (g/cm^3)

which the data were ranked (primary relationship) but also between OR and the remaining two factors. The significance level, and coefficient of determination (r^2) for each of these relationships is shown in Table 11. The values for each primary relationship considered in (i), (ii) and (iii) above are emphasised by being enclosed in boxes.

Examination of Table 11 reveals that when the data were ranked on LW there was a relationship of similar significance between OR and each of the three factors. This occurred at each of the three times of observation, with significant relationships ($P < 0.05$) in both March 1972 and March 1973 and no apparent relationship in September 1972. When ranked on BS there was no relationship of OR with any of the factors in either September 1972 or March 1973, but in March 1972, while there was no relationship with BS or LW, there was a significant relationship with BC ($P < 0.05$). When the data were ranked on BC there were similar relationships between OR and each of the factors in March 1972 only. In September 1972 there was a similar significant relationship with both LW and BC ($P < 0.05$) but no apparent relationship with BS. In March 1973 there were similar significant correlations between OR and both LW and BS ($P < 0.05$), but not BC.

In view of the number of similar relationships between OR and each of the three factors, linear correlations were also calculated directly between each factor. The significance level, and correlation coefficient (r) for each correlation is shown in Table 12. These analyses showed that when the data were ranked on LW there was a highly significant correlation between each of the factors at each time of observation. When the data were ranked on BC there was a highly significant correlation between LW and BC (but not the other two combinations) at each time. When ranked on BS the correlations varied between times of observation.

Table 11. Summary of regression relationships (coefficient of determination - r^2, significance) in March 1972, September 1972 and March 1973 between adjusted ovulation rate (OR), adjusted wool-free, fasted, liveweight (LW), adjusted body size (BS) and adjusted body condition index (BC) for the data ranked and grouped on the adjusted value of either liveweight, body size or body condition.

Relationship	Adjusted data ranked and grouped on					
	Liveweight[a]		Body size[a]		Body condition[a]	
	r^2	Sig.	r^2	Sig.	r^2	Sig.
(a) *March 1972*						
OR - LW	0.57	*	0.46	N.S.	0.33	N.S.
OR - BS	0.53	*	0.41	N.S.	0.003	N.S.
OR - BC	0.60	*	0.53	*	0.42	N.S.
(b) *September 1972*						
OR - LW	0.25	N.S.	0.02	N.S.	0.62	*
OR - BS	0.22	N.S.	0.03	N.S.	0.21	N.S.
OR - BC	0.26	N.S.	0.004	N.S.	0.64	*
(c) *March 1973*						
OR - LW	0.65	*	0.26	N.S.	0.50	*
OR - BS	0.61	*	0.33	N.S.	0.53	*
OR - BC	0.70	*	0.00	N.S.	0.40	N.S.

a n = 8
* $P < 0.05$

Table 12. Summary of correlation relationships (correlation coefficient - r , significance) in March 1972, September 1972 and March 1973 between adjusted wool-free, fasted, liveweight (LW), adjusted body size (BS) and adjusted body condition index (BC) for data ranked and grouped on the adjusted value of either liveweight, body size or body condition.

	Adjusted data ranked and grouped on					
Relationship	Liveweight[a]		Body size[a]		Body condition[a]	
	r	Sig.	r	Sig.	r	Sig.
(a) *March 1972*						
LW - BS	0.99	***	0.99	***	0.66	N.S.
LW - BC	0.98	***	0.74	*	0.99	***
BS - BC	0.93	***	0.67	N.S.	0.52	N.S.
(b) *September 1972*						
LW - BS	0.99	***	0.99	***	0.66	N.S.
LW - BS	0.98	***	0.80	*	0.99	***
BS - BC	0.93	***	0.73	*	0.54	N.S.
(c) *March 1973*						
LW - BS	0.95	***	0.99	***	0.66	N.S.
LW - BC	0.98	***	0.58	N.S.	0.98	***
BS - BC	0.90	**	0.52	N.S.	0.10	N.S.

a $n = 8$

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

The only consistent correlation ($P < 0.001$) was between LW and BS. The remaining two combinations were related in September 1972 ($P < 0.05$) but unrelated in March 1973, while in March 1972 LW and BC were related ($P < 0.05$) but BS and BC were apparently not correlated.

(b) Data for individual ewes (ungrouped data)

The individual values of each factor, adjusted for the effect of treatment, were examined by partial correlation analysis. The 'r' value, 'F' value and significance level for each of these relationships in March 1972, September 1972 and March 1973 is shown in Table 13.

At each time of observation there were significant correlations between OR and both LW and BC, and between LW and both BS and BC, but not between OR and BS. When liveweight was held constant there was no apparent (partial) correlation between OR and either BS or BC.

In contrast to the within-time analyses there was a significant correlation ($P < 0.05$) between OR and BS when the ovulatory performance of each ewe was accumulated either over all three times, or over March 1972 and March 1973 only.

2. DISCUSSION

The two methods of examining the data (grouped, ungrouped) both revealed that, at each time, OR and LW was related and OR and BS was not related. However, both analyses showed that BS was associated ($P < 0.05$) with ovulatory performance accumulated either over all three times, or over March 1972 and March 1973 only. The apparent relation between OR and BC varied between the two types of analysis. On a grouped basis there was a significant correlation ($P < 0.05$) in September 1972 only, while on an ungrouped basis there was an association ($P < 0.01$) at

Table 13. Partial correlation analysis of the relationships between adjusted[a] ovulation rate (OR), adjusted liveweight (LW), adjusted body size (BS) and adjusted body condition index (BC) in March 1972, September 1972 and March 1973.

	r Value			d.f.	F Ratio			Significance		
	M72	S72	M73		M72	S72	M73	M72	S72	M73
(a) *Correlations*										
OR - LW	0.20	0.15	0.20	201	8.17	4.65	8.00	**	*	**
OR - BS	0.11	0.04	0.12	201	2.29	0.27	2.99	N.S.	N.S.	N.S.
OR - BC	0.19	0.19	0.18	201	7.17	7.51	6.97	**	**	**
LW - BS	0.75	0.70	0.70	201	255.3	196.4	196.8	***	***	***
LW - BC	0.74	0.78	0.80	201	248.6	310.6	361.2	***	***	***
(b) *Partial correlations*										
OR - BS (LW constant)	0.06	0.10	0.02	200	0.83	1.95	0.11	N.S.	N.S.	N.S.
OR - BC (LW constant)	0.06	0.12	0.05	200	0.70	2.79	0.40	N.S.	N.S.	N.S.
OR - BS (BC constant)	0.09	0.02	0.10	200	1.50	0.06	1.91	N.S.	N.S.	N.S.
OR - LW (BC constant)	0.09	0.004	0.08	200	1.67	0.003	1.39	N.S.	N.S.	N.S.

[a] Adjusted for different in treatment means.

each of the three times.

Thus, in this study, the level of ovulatory performance was clearly and consistently associated with within-flock differences in liveweight, generally associated with differences in body condition and only slightly, if at all, associated with differences in body size.

Both methods of analysis revealed a high association between both LW and BS, and LW and BC, at each of the three times of examination. There was no apparent relationship between BS and BC except for the ungrouped March 1973 data and the September 1972 data ranked and grouped on body size, when there was a significant association ($P < 0.05$). This intermittently occurring significance may reflect a weak underlying relationship. Such a relationship should probably be expected, for some ewes are likely to be small and of low body condition because they are unthrifty animals. They would not cover the range of body condition expected among healthy, genetically small, ewes of similar size. An association among the smaller, low body condition ewes may be sufficient, on some occasions, to cause an apparent correlation among the whole flock.

The 1.3 per cent to 1.5 per cent increase in OR for each 1 kg increase in LW observed during autumn in this study confirms almost exactly the 1.3 per cent increase reported by Fletcher (1971). There was probably a similar relationship in early spring also, although it was more variable with the ungrouped data being correlated at a lower level of significance ($P < 0.05$ in lieu 0.01) and the grouped data being not significantly related.

At each time of observation, the partial correlation analysis showed that OR and BC were not significantly associated when LW was held constant. Conversely there was not a significant association between

OR and LW when BC was held constant. It seems that OR was related to either LW or BC. This view is consistent with the analysis of the grouped data where, at each time, there was a highly significant linear regression relationship between LW and BC when the data were ranked on either LW or BC. While OR could be predicted from either measurement the relative ease of measuring LW compared with BC, and the possibility of a weak relationship between OR and BS being reflected in LW, both suggest that LW is the better variable to measure as an indicator of OR.

How good is the correlation between the proportion of fat in the animal and body condition index (i.e. BC) compared with that of other measures of body condition? Guerra, Thwaites and Edey (1972a) found that BC was as well associated with % chemical fat in the empty body as either palpated condition score (as described by Russel, Doney and Gunn, 1969) or direct measurement of the subcutaneous fat depth over the backbone above the first lumbar transverse process. They also reported an equally strong association with liveweight. While Russel *et al.* (1969) found that % chemical fat was more highly correlated with palpated condition score than liveweight, the latter was still highly significantly correlated and similar to that reported by Guerra *et al.* (1972a). In the present study, the association between % fat and both BC and LW was calculated for both the Field and Variable groups at Times 5 (October) and 8 (April). Considered over the four instances % fat was similarly, moderately, correlated with both BC (one $P < 0.001$, one $P < 0.01$, two $P < 0.05$) and LW (one $P < 0.001$, two $P < 0.01$, one $P < 0.05$). It appears that BC (index) is usually as well correlated with the proportion of fat in the animal as either palpated condition score, the depth of back-fat, or liveweight.

However, it is well to note that these various body condition estimates should not be regarded as synonymous with proportion of fat. For, while the associations between them and % chemical fat (or body fat) are generally significant at the 0.1 per cent level of probability, they are not especially tight associations; the correlation coefficients are in the range 0.5 to 0.8 for data from 15 to about 50 animals. In this situation the possibility exists that while OR was not directly associated with BC (other than via the relationship with LW) it could have been associated with a more accurate measure of body condition, say, % chemical fat.

WITHIN-FLOCK RELATIONSHIPS

(b) WATER TURNOVER

E. WITHIN-FLOCK RELATIONSHIPS WITH OVULATION RATE (b) WATER TURNOVER

Water turnover was measured in the same ewes and at the same nine Times as for the various body components. There were 70 complete sets of data. (See Body Composition and Water Turnover section). In addition, measurements were made on all of the Field and Variable ewes in October 1972 (Time 5) and April 1973 (Time 8).

These data were examined to ascertain, firstly, whether there was evidence of a relationship between ovulation rate and water turnover and, secondly, whether there were any animals that consistently had a higher or lower than average rate of water turnover. The first relationship was examined using regression analysis within each of the two groups (Field, Variable) at both Times (5 and 8). The relationship was also examined by single way analysis of variance of the mean rate of water turnover of ewes having two, one or nil ovulations. The second relationship was examined by visual comparison of the plotted values of turnover for each of the 70 ewes examined at each of the nine Times throughout the experiment and also by rank correlation analysis within each of the treatment groups (Steele and Torrie (1960), p. 409).

1. RESULTS

(a) Water turnover and level of ovulation

The data for the Variable and Field groups at both Time 5 and Time 8 was examined within treatment group. This was done by ranking the ewes in descending order of their rate of water turnover and then grouping and ranked turnover and ovulation data into five blocks. This procedure provided five pairs of mean values that were examined using regression analysis. These data are shown in Table 14.

Table 14. The mean rate of water turnover (ml/kg$^{0.82}$/24 h) and ovulation rate (OR) for each quintile of (a) the Variable and Field groups at Times 5 and 8 (unadjusted data), and (b) the Variable and Field groups combined at each Time (adjusted data[a]).

Quintile	Time 5						Time 8					
	Variable			Field			Variable			Field		
	No.	Turnover	OR	No.	Turnover	OR	No.	Turnover	OR	No.	Turnover	OR
(a) *Unadjusted data*												
1 (highest)	10	147.6	1.00	11	167.8	1.18	9	139.9	1.33	11	265.2	1.55
2	10	125.9	1.10	11	138.9	1.18	10	119.6	1.30	11	210.3	1.36
3	10	115.8	1.20	11	127.9	1.27	10	110.0	1.20	11	190.2	1.73
4	10	109.5	1.20	11	112.1	1.36	10	95.5	1.20	11	172.0	1.09
5 (lowest)	10	99.3	1.20	11	101.5	1.09	9	70.5	1.33	11	149.3	1.64

(b) *Adjusted data*[a]	Time 5			Time 8		
	No.	Turnover	OR	No.	Turnover	OR
1 (highest)	21	158.3	1.09	20	207.9	1.48
2	21	132.6	1.15	21	168.0	1.33
3	21	122.1	1.24	21	155.0	1.26
4	21	112.2	1.31	21	136.0	1.37
5 (lowest)	21	99.1	1.12	20	111.4	1.36

[a] Values for individual ewes adjusted for differences in treatment means.

In order to increase the number of sets of data in each block the data for both treatment groups were combined within each season. The individual values for both water turnover and ovulation were adjusted for difference in treatment means. The ewes were ranked in order of their adjusted water turnover and then the same procedure was followed as for the individual groups. The mean values for the pairs of adjusted turnover and adjusted ovulation data (adjusted data) are also shown in Table 14.

There was no evidence of a regression relationship between ovulation rate (y) and water turnover (x) either in the unadjusted data for the Field group in September 1972, for either group in March 1973, or in the adjusted data for the combined groups at either season. There was a statistically significant linear regression relationship ($P < 0.05$) among the Variable ewes in September 1972 of $y = 1.69 - 0.0046x$.

The rate of turnover of ewes with either two, one or nil ovulations was examined for both the Variable and Field ewes in both September 1972 and March 1973. The data were first examined within each age group of ewes (1967 ewes, 1968 ewes) using t-test analysis. As there were no significant differences between the age groups the data were combined. The average rate of water turnover for the combined age groups is shown in Table 15. Analysis within each treatment group did not reveal any instance where the mean rate of water turnover was significantly different at different levels of ovulation.

(b) Consistency of rate of water turnover throughout the experiment

The consistency of the rate of water turnover of individual ewes, relative to other ewes in the same group, was examined by plotting

Table 15. The mean rate of water turnover (ml/kg$^{0.82}$/24h) of ewes among the Variable and Field groups that had two, one or nil ovulations in September 1972, or March 1973.

Number of ovulations	September 1972				March 1973			
	Variable		Field		Variable		Field	
	No.	Turnover	No.	Turnover	No.	Turnover	No.	Turnover
2	10	119.4 (6.7)[a]	17	128.5 (6.0)	13	107.1 (7.8)	26	199.0 (8.5)
1	37	118.8 (2.8)	33	132.5 (4.4)	35	107.8 (3.8)	29	196.0 (8.2)
0	3	130.5 (13.0)	5	114.8 (10.4)	-	-	-	-

[a] Standard error of mean.

the turnover of each ewe at each of the nine Times. Three graphs were plotted, with each graph including all 70 ewes but only three Times (Times 0, 1 and 2; Times 3, 4 and 5; Times 6, 7 and 8). This examination revealed few animals with an apparently consistent relative rate of turnover. There were two ewes almost always the highest of their group and one almost always lowest. There were a further six or seven that were fairly consistently high or low for three or four of the nine Times.

In addition to the visual examination the data were examined within treatment groups using Spearman's rank correlation analysis (Steele and Torris, p. 409). The resultant values are distributed as Student's t with n-2 degrees of freedom. The 36 values (and significance levels) for each of the Low, High, Variable and Field groups are shown in Tables 16a to 16d, respectively.

There were few instances of significant correlation between the rankings for either the Low, High or Field groups. (Low, 4, including one negative; High, 3; Field, 4, including 2 negative). There were 12 significant combinations for the Variable group. Six of the combinations were for successive observations and a further three were for Times separated by only one observation.

2. DISCUSSION

The most important finding of the study of water turnover and ovulation was that there was little evidence of consistency in the relative levels of turnover between the different Times of measurement. At successive Times there were marked changes both in the mean rate of turnover, and in the rate of individual ewes relative to the mean of their group. Thus, of the two factors being considered, one had a low level of consistency (repeatability), while the other, ovulation rate, probably

Table 16a. Matrix of t-values for Spearman's rank correlation coefficients for the rate of water turnover (ml/kg$^{0.82}$/24 h) of Low ewes (n = 18) at Times 0 (T_0) to 8 (T_8).

	T_0	T_1	T_2	T_3	T_4	T_5	T_6	T_7
T_1	2.50 *							
T_2	-0.78 N.S.	0.09 N.S.						
T_3	1.12 N.S.	2.61 *	-0.21 N.S.					
T_4	-4.17 *	0.25 N.S.	0.50 N.S.	0.83 N.S.				
T_5	0.45 N.S.	-0.30 N.S.	1.47 N.S.	1.67 N.S.	0.51 N.S.			
T_6	0.35 N.S.	1.45 N.S.	0.35 N.S.	2.13 *	1.11 N.S.	1.52 N.S.		
T_7	0.83 N.S.	0.99 N.S.	-0.07 N.S.	0.91 N.S.	-0.33 N.S.	0.67 N.S.	1.84 N.S.	
T_8	0.44 N.S.	-0.62 N.S.	-0.42 N.S.	1.47 N.S.	0.44 N.S.	0.72 N.S.	1.43 N.S.	1.37 N.S.

N.S.	Not significant
*	$P < 0.05$

Table 16b. Matrix of t-values for Spearmn's rank correlation coefficients for the rate of water turnover (ml/kg$^{0.82}$/24 h) of High ewes (n = 18) at Times 0 (T_0) to 8 (T_8).

	T_0	T_1	T_2	T_3	T_4	T_5	T_6	T_7
T_1	0.73 N.S.							
T_2	0.95 N.S.	1.20 N.S.						
T_3	-1.15 N.S.	-1.53 N.S.	-0.39 N.S.					
T_4	1.23 N.S.	-0.56 N.S.	1.52 N.S.	0.08 N.S.				
T_5	0.89 N.S.	0.97 N.S.	0.11 N.S.	0.59 N.S.	1.30 N.S.			
T_6	0.23 N.S.	0.46 N.S.	0.33 N.S.	1.16 N.S.	1.90 N.S.	1.59 N.S.		
T_7	1.84 N.S.	0.21 N.S.	2.24 *	0.42 N.S.	1.76 N.S.	0.31 N.S.	1.55 N.S.	
T_8	1.01 N.S.	0.90 N.S.	0.60 N.S.	0.08 N.S.	1.19 N.S.	-1.18 N.S.	2.73 *	2.31 *

N.S. Not significant
* $P < 0.05$

Table 16c. Matrix of t-values for Spearman's rank correlation coefficients for the rate of water turnover (ml/kg$^{0.82}$/24 h) of Variable ewes (n = 16) at Times 0 (T_0) to 8 (T_8).

	T_0	T_1	T_2	T_3	T_4	T_5	T_6	T_7
T_1	1.55 N.S.							
T_2	0.91 N.S.	3.10 **						
T_3	1.69 N.S.	3.12 **	2.31 *					
T_4	1.28 N.S.	1.41 N.S.	1.08 N.S.	2.78 *				
T_5	1.16 N.S.	1.84 N.S.	0.50 N.S.	2.13 N.S.	1.61 N.S.			
T_6	1.62 N.S.	1.06 N.S.	0.42 N.S.	1.02 N.S.	1.00 N.S.	4.95 ***		
T_7	0.40 N.S.	1.70 N.S.	2.49 *	1.51 N.S.	2.17 *	2.32 *	2.83 *	
T_8	1.09 N.S.	1.65 N.S.	2.74 *	1.24 N.S.	0.38 N.S.	0.56 N.S.	2.46 *	3.69 **

N.S.	Not significant
*	$P < 0.05$
**	$P < 0.01$
***	$P < 0.001$

Table 16d. Matrix of t-values for Spearman's rank correlation coefficients for the rate of water turnover (ml/kg$^{0.82}$/24h) of Field ewes (n = 18) at Times 0 (T_0) to 8 (T_8).

	T_0	T_1	T_2	T_3	T_4	T_5	T_6	T_7
T_1	-0.35 N.S.							
T_2	0.23 N.S.	1.34 N.S.						
T_3	0.39 N.S.	-0.09 N.S.	0.87 N.S.					
T_4	1.47 N.S.	0.62 N.S.	0.34 N.S.	1.10 N.S.				
T_5	0.51 N.S.	1.59 N.S.	0.31 N.S.	-0.82 N.S.	0.16 N.S.			
T_6	0.91 N.S.	-0.78 N.S.	-2.16 *	-0.17 N.S.	1.77 N.S.	0.92 N.S.		
T_7	0.60 N.S.	-1.08 N.S.	-0.05 N.S.	0.37 N.S.	1.33 N.S.	-1.55 N.S.	1.87 N.S.	
T_8	0.19 N.S.	-0.03 N.S.	-0.98 N.S.	1.68 N.S.	1.92 N.S.	-2.66 *	2.63 *	3.41 *

N.S. Not significant
* $P < 0.05$

had a repeatability of about 0.5 (Carrick, Oldham and Lindsay, 1976). In this circumstance it is not surprising that no relationship was detected between turnover and ovulation rate. However, it should be noted that there were several features of the experimental design, dictated by other considerations in the overall experiment, that could have increased the amount of variation and thereby had a masking effect on the detection of a relationship.

Firstly, the estimates of mean ovulation rate were based on minimal numbers of observations (9 to 21 for regression analysis). As this variate is basically binomial in nature the estimates of ovulation rate were probably subject to a considerable error. While the turnover estimates were based on the same number of animals the error associated with those estimates would most likely have been less, for turnover is a continuous variate. Secondly, only single sets of ovulation and turnover data were used in an attempt to detect a relationship between the two variates. No account was taken of short term changes or variation in either variate. Repeated observations of ovulatory performance at two or three successive oestrous cycles would improve the reliability of the ovulation data. The present study indicates it is unlikely that repeated observations of turnover would significantly improve the reliability of the turnover estimates. However, this relates to relatively infrequent repetition - more frequent repeated measurement may reduce the variation. Thirdly, the turnover estimates were made shortly after the ewes were examined by laparoscopy. Individual differences in response to this examination may temporarily influence the rate of water turnover of some ewes.

There is a fourth feature that should be considered, namely, the effect of the procedure used to estimate the rate of water turnover per unit of liveweight. In particular, the ewes were subjected to a 42 to

44 hour fast before the period of water turnover measurement started, and the liveweight used to calculate turnover per unit of liveweight was recorded after 22 hours of that fast. A small set of observations showed that in this situation the ewes usually lost 5 to 6 per cent of their liveweight in 22 hours and 6 to 8 per cent in 42 hours. About three-quarters of the weight loss was regained within seven hours of being returned to feed and water while the remainder was regained during the following two to five days - Low ewes took the longest time.

This procedure affects the calculated rate of water turnover per unit of liveweight compared with the rate that would be determined if fasting did not occur. The initial TOH concentration is increased, thereby increasing the apparent rate of water turnover (% per day). However, the value of total body water is lowered by the fasting. These two effects tend to cancel each other. In addition the turnover per unit liveweight (ml/kg$^{0.82}$/24 h) is calculated using the fasted liveweight. This acts to increase the final estimate. The overall effect is that for a 22-hour fasted liveweight loss of 5 per cent the turnover per unit liveweight is over-estimated by about 1.5 per cent when the daily turnover is 30 per cent, 4 per cent when turnover is 15 per cent, 6 per cent when 10 per cent per day, and 14 per cent when 5 per cent per day. The corresponding over-estimates if there is a 10 per cent liveweight loss due to fasting are 3.5 per cent, 9 per cent, 15 per cent and 31 per cent, respectively.

On this basis the distorting effect of the procedure adopted would have been more marked in the rank correlation analysis than in the regression analyses, for in a number of instances the daily turnover rates covered the range from less than 5 per cent to greater than 10 per cent Thus the lower rates of turnover would have been markedly over-estimated and the range of values compressed at the lower end. In most cases the data examined by regression analyses were derived from ewes that had turnover rates of greater than 10 per cent per day: there were no rates of less than 5 per cent.

Insufficient ewes exhibited a degree of consistency of water turnover to allow a sound statistical comparison between the ovulation rate of those with high turnover and those with low turnover. The turnover ranking (at each of the nine Times) and ovulatory performance of those chosen in shown in Appendix Table 9. The ovulation rate of those (n = 8) with consistently high turnover (1.13) was not significantly lower than that of those (n = 9) with low turnover (1.19).

The detection of a significant negative linear relationship between ovulation rate and water turnover among the Variable ewes in September 1972 was surprising in view of the inconsistency considered above. The overall greater degree of consistency among these ewes compared with the Field ewes (as shown by rank correlation analysis) could perhaps be significant. The higher consistency might have decreased the variation enough to allow a relationship to be detected. However, as this set of data were out of line with the other five sets, the regression was weak and negative, and the ovulation rates were low and therefore increasingly inaccurate, it is most likely that the apparent relationship was an isolated chance occurrence.

3. SUMMARY (WITHIN-FLOCK RELATIONSHIPS WITH OVULATION RATE)

(1) Ovulation rate was positively associated with within-flock differences in both liveweight and body condition index (liveweight/body size) at ovulation, but the associations were not independent. At constant liveweight there was not a significant association with body condition, and at constant body condition there was not an association

with liveweight. Although there was not a significant association between ovulation rate and body size at any of the three Times of observation there was a weak association when ovulatory performance was summed over all Times, or over the two March observations.

Liveweight appears to be a better measurement to use as an indicator of ovulation rate than body condition as it was equally well associated with ovulation rate, is more easily measured, and is likely to reflect any weak effects of body size on ovulation.

(2) The rate of water turnover of individual ewes generally varied greatly between successive measurements, both in terms of absolute level, and relative to other ewes in the same group. Accordingly there were only few ewes that had a fairly consistent relative level of turnover. As may be expected in view of this inconsistency no general relationship was detected between ovulation rate and water turnover. The negative relationship detected among one group on one occasion was most likely a chance occurrence.

GENERAL DISCUSSION

V. GENERAL DISCUSSION

Discussion in this chapter is restricted to comparing certain points raised in this study with other generally similar studies that differ in location and/or type of ewe; to considering the interrelation of points arising in several sections of this study; and, retrospectively, to reviewing and considering certain literature in the light of happenings in the study. Discussion relating specifically to one aspect of the study, namely comparison with previous experiments conducted using the same flock of Koonoona ewes, is contained in the relevant section of the Results and Discussion chapter.

(a) Oestrus and season

The oestrous behaviour of the Koonoona ewes observed in this study can be compared with previous Australian studies of Merino ewes. Kelley and Shaw (1943) observed 'South Australian' ewes (bred over many years in New South Wales from 'Koonoona' and 'North Bungaree' rams) at the McMaster Field Station, Badgery's Creek west of Sydney, while Riches and Watson (1954) studied Peppin Merino ewes at Cunnamulla in western Queensland.

While the occurrence of oestrus to day 35 (or 28) can be compared directly with data provided by Riches and Watson (1954), comparison of the incidence to day 16 can only be made with several assumptions. Firstly, that in the present study the sudden introduction of rams did not stimulate oestrous behaviour until one oestrous cycle later, and therefore the ewes detected in oestrus to day 16 can be considered as those cycling naturally (i.e. unaffected by the presence of rams).

Secondly, that as the observations of both Kelley and Shaw (1943) and Riches and Watson (1954) were related to ewes continuously associated with rams for many months the oestrous activity recorded each month would also be that occurring naturally (Lishman, 1969).

The comparable data of Kelley and Shaw (1943), Riches and Watson (1954) and the Field ewes in the present study are shown in Table 17. The somewhat lower incidence observed in the present experiment may be a consequence of using the incidence to day 16 after the introduction of rams as an estimate of that observed during a month if the ewes had been continuously associated with rams.

Consideration of the data in Table 17 shows clearly that in each experiment the incidence of oestrus to day 28 (or one month) after the introduction of rams was only slightly affected by the season of joining. On the other hand it is equally clear that in the absence, or effective absence, of ram stimulation almost all of the ewes experienced oestrus in March but substantially fewer did during September. While the specific comparisons indicate that each of the three flocks of ewes behaved similarly it should not be assumed that the overall oestrous behaviour of Koonoona and Peppin ewes is the same. In my previous study (unpublished) I found that the lowest incidence to day 28 among the Koonoona ewes occurred in September-October when 75 per cent were detected in oestrus. However, in two successive years the lowest incidence of oestrus detected by Riches and Watson (1954) among their Peppin ewes was 80 per cent in October and 30 per cent in December: in neither year was the lowest incidence recorded during September. Peppin ewes may have a deeper, and possibly later, anoestrous period than Koonoona ewes. Dun, Alexander and Smith (1966) found that Peppin and South Australian strains exhibited different seasonal reproductive

Table 17. Comparative oestrous data (% incidence during a one month period) for the Field group of this study and for broadly comparable groups studied by Kelley and Shaw (1943) and Riches and Watson (1954).

	Incidence of oestrus (%)	
	Rams continuously with ewes	Rams introduced to ewes
(a) Field ewes		
March, 1972	86[a]	98[b]
September, 1972	21	86
March, 1973	83	91
(b) Kelley and Shaw (1943)		
September, 1937	0	-
March, 1938	95	-
September, 1938	30	-
March, 1939	100	-
September, 1939	45	-
March, 1940	100	-
September, 1940	24	-
March, 1941	100	-
September, 1941	45	-
(c) Riches and Watson (1954)		
March, 1942	89	100
September, 1942	20	90
March, 1943	85	100
September, 1943	65	90

[a] For the Field ewes the incidence is that observed during the first 16 days of joining.

[b] For the Field ewes the incidence is that observed during the first 28 days of joining.

performance and suggested that the difference may be due to selection over 120 years or more for a particular time of joining. While they referred to a different strain of South Australian and Peppin ewe there may be similar differences between Koonoona ewes and the Peppin ewes studied by Riches and Watson.

(b) Oestrus and treatment

In practical terms the treatments imposed had little effect on oestrous behaviour except during September when there was a lower incidence to day 16 among the Field ewes, compared with the pen-fed ewes. This situation remains a point of interest, although it is largely academic, as in practice such an effect could be reduced to insignificance by extending the joining period by the length of one oestrous cycle. As pointed out in the Oestrus section of the Results and Discussion Chapter differences in either the proximity of rams, or the level of nutritional, or non-nutritional, stress do not appear to offer an explanation. While the precise explanation must remain undefined the amount of between-year variation in the incidence of oestrus reported by Kelley and Shaw (1943) and Riches and Watson (1954) (Table 12) may provide a pointer, as it was as large as the treatment effect in the present study. In some years they observed an incidence similar to that among the Field ewes (about 20%) and in others an incidence similar to the pen-fed groups (about 45%). Consideration of their data for the whole year shows that this variation resulted largely from the ewes becoming anoestrus at different times in different years: sometimes by September and sometimes by October. This situation suggests that the lower incidence among the Field ewes could have been the consequence of a slight alteration to the timing of the anoestrous period of these ewes compared with the pen-fed ewes. It also suggests that the difference observed between the pen-fed and field grazed ewes in the present study is likely to be inconsistent between years. If this is correct, it appears that the variation is likely to result from the interaction of a number of factors that individually have only a small effect.

(c) Ovulation and treatment

During autumn there appeared to be a greater incidence of multiple ovulation among the Field ewes than either the Variable ewes or all the pen-fed groups, when compared on the basis of either liveweight, or body condition index, at ovulation. During spring, there was a less marked difference when compared on a liveweight basis and no apparent difference when compared on the basis of body condition index. It was suggested earlier, in the Ovulation section of the Results and Discussion chapter, that the higher incidence during autumn might have been associated with differences in body composition.

Unfortunately, although body composition was measured specifically in the hope that group differences in fat, protein or water would provide a feasible explanation if this type of difference should occur, the data collected to not appear to provide a substantial explanation. However, in view of reports relating feed quality and ovulation published since the experiment began (Lightfoot and Marshall, 1974; Marshall and Lightfoot, 1974; Knight, Oldham and Lindsay, 1975; Arnold and Charlick, 1976; Lindsay, 1976), the weak relationship observed between the incidence of multiple ovulation and weight of protein assumes greater significance. As these reports quite clearly show that differences in the quality of the diet offered to ewes can alter the level of ovulation within seven to ten days and that this can occur without a significant concurrent increase in liveweight, the relationship observed in this study may reflect a closer relationship of ovulation with the protein status of the ewes than with their fat status, or possibly their body condition status; at least during autumn. Although this situation is consistent with the recently reported effect of feed quality on ovulation it is not necessarily supportive. However, in view of the uncertainty about whether the response to feed quality is due to the protein or energy content, or to some other fraction, of the feed, the present observation adds a little weight to the view that the response is related to protein content.

While the recently reported responses have related to lupin supplementation of ewes grazing poor quality pasture, or cereal stubble, Torrell *et al.* (1972b) reported an improved performance among ewes grazing improved pasture compared with similar ewes grazing native pasture. Thus it is reasonable to assume that there could be a similar response to quality differences between green and dry feed or, as in this study, between green, or even dry, pasture and a hay/grain ration (see also following section - 'dynamic response to flushing and feed quality').

It is therefore relevant to note that during the present study there were sufficient falls of rain early in February 1973 to germinate annual pasture species (*Hordeum* sp., *Polygonum* sp., *Trifolium subterranean*) and to provide a substantial 'green pick' for the Field ewes during the last four weeks before the ovulation observations in March, 1973. While no measurements were made of the quality of the feed it is almost certain that the protein content of the diet increased considerably as the green feed became available. Thus the ovulatory performance of the Field ewes could have increased above that expected on a liveweight basis because the feed available was of a higher quality. It is likely that there was either less, or no, difference in feed quality before the March 1972 observations as there was no green feed available then. The apparently higher performance of the Field ewes at that time (March 1972) could have been the result of either a depressed performance among the Variable ewes following a period of severe undernutriton, as mentioned previously, or a combination of undernutrition and feed quality effects. As, when the data were plotted and compared on the basis of either liveweight or body condition index (see Figures 10, 11 and 12), the Variable group's performance was not as obviously low, as the Field group's was high, it is more likely that there was a combined effect.

There is a potential inconsistency with the suggested effect of feed quality. Why, when the respective diets available were similar at both times, should the availability of green feed apparently produce a response in ovulatory activity in March but not in September? Several possible effects, acting either singly or in some combination, can be suggested to explain the inconsistency. Firstly, the absolute level of response to a given difference in feed quality may be affected by the general level of sexual activity of the flock at that time. The response may be smaller when the level of activity is lower, as it was in September. Secondly, the level of response could be affected by the nutritional status of the animals. Lindsay (1976) has postulated that ovulatory activity may be related to "the sum of endogenous katabolic sources of nutrients and uptake of exogenous nutrition from the gut". This hypothesis could be interpreted as implying that changes in the quality of the exogenous nutritional intake affect ewes more when they are in either poor, or falling, condition, than when they are in either good, or rising, condition, for in the former situations they are more reliant on the exogenous source of nutrition. An effect of this nature could explain the apparent lack of response to the green feed available to the Field ewes before September, 1972, for at that time the ewes were rising in condition whereas in March they were falling in condition. A third possibility is that the ovulatory response to differential levels of feed quality is more marked immediately following the change in nutritional conditions and that if the levels are maintained the response decreases with time. Thus, following about four months of grazing on green feed, the response in September may have been minimal.

(d) Dynamic response to flushing and feed quality

The implications of a feed quality effect on ovulation can be considered in relation to the conflicting evidence in the literature concerning the effects of flushing on ovulation. For the situation where a difference in feed quality affects the level of ovulation, without causing any significant change in liveweight, can be considered as a special case of a dynamic effect of flushing in which there is insufficient time for a noticeable liveweight response to occur. In this situation the static effect of liveweight is the same for both groups (as they are nominally of equal weight) and the improved performance of the group fed a higher quality feed is equivalent to a dynamic effect. This reasoning suggests the possibility that variation in feed quality between the flushed and control treatments may provide an explanation for why the literature concerning the effects of flushing is notable for its relatively even distribution of reports stating that there were, or were not, dynamic effects of flushing over and above that expected on a liveweight basis (static effect).

With this in mind I examined the information available regarding the feeding procedures adopted in a number of flushing experiments. The description of the feed and feeding procedure adopted, together with the breed and number of sheep observed, the unit of measurement, the overall flushing effect (static and dynamic effect), the calculated dynamic effect and the general condition of the ewes at the time of flushing is summarised for each report in Table 18. The dynamic effect of flushing was not always stated. In these circumstances I adjusted the overall flushing effect to allow for differences in liveweight at ovulation, or mating, on the basis of an increase of 10 per cent in ovulation and 6 per cent in multiple births for each 4.5 kg (10 lb.) increase in mean liveweight.

The most striking features revealed by this examination were the scanty descriptions given of the feeding regimes (in some instances there was none) and the number of experiments in which different feeds were offered to the flushed animals, than to the control animals. In most instances the feed description given in Table 18 has been curtailed little from that given in the original reports. Nineteen of the 32 experiments reported in the 13 papers considered were conducted with different feed being offered to the flushed ewes than to the control ewes. In these experiments the flushed ewes probably received more feed of higher quality. In contrast, seven experiments were conducted using the same feed for both the control and flushed groups. In these experiments the flushed groups simply received more feed (of the same quality). Of the remaining six experiments two were designed so that various amounts of a supplementary feed were offered in addition to paddock grazing and in four instances no feeding details were stated.

The calculated dynamic effect, on average, was lower among the experiments conducted using different amounts of the same feed than among those using different qualities of feed, but the difference was not clear-cut. The responses observed by Fletcher (1971) were substantially lower, but those observed by Gunn and Doney (1975) and Killeen (1967) were similar to the average response observed among all the experiments

Table 18. Summary of details of 'flushing' experiments showing feeding treatment, breed and number of ewes, unit of measurement, total flushing effect, calculated dynamic flushing effect and the condition of the ewes at flushing.

Feeding treatment (a) Control (b) Flushing	Breed	Group size	Type of observation	Total effect (%)	Calculated dynamic effect[a] (%)	Condition at flushing
1. *Underwood and Shier (1941)*						
At first (a) ? (b) cereal stubble then later (a) self-sown oats & subterranean clover (b) oat stubble, unharvested peas	BL X Merino	350	births/ewe present at lambing	20	12	poor/medium
2. *Darrock, Nordskog and Van Horn (1950)*						
(a) pasture	Columbia	115 approx	birth/ewe present	3	3	medium
(b) pasture plus ½ lb of beet pulp pellets/day		115 approx		16	15	poor
3. *Allen and Lamming (1961)*						
(a) bare pasture (b) flushing pasture (rye grass, white clover)	Kerry Hill	6	ovulation/ ewe ovulating	55	37-46	very poor
4. *McInnes and Smith (1966)*						
(a) natural pasture (barley grass, spear grass) (b) oats	Merino	21 approx	births/ewe lambing	10-12	10-12	various
5. *Wallace (1951)*						
(a) pasture considered to cause neither gain nor loss of weight	?	150	births/ewe lambing	19	12	poor/medium
(b) best pasture available		154	"	10	5	poor/medium
6. *Tribe and Seebeck (1962)*						
(a) dry, meadow pasture (b) oats, dry clover pasture, *ad lib.* meadow hay (11% C.P.)	BL X Merino	160 151	lambing % (/ewe present?)	13	9	medium (?)
(a) dry meadow pasture (b) green rape crop, dry clover pasture	BL X Merino	144 147	lambing % (/ewe present?)	9	5	medium (?)
7. *Hulet et al. (1962)*						
(a) dry pasture, hay (b) dry pasture, hay, oat supplement for 17 days pre-joining	Columbia & Targhee	100 approx	births/ewe present at lambing	16-17	15-16[b]	medium (?)
(a) dry pasture, hay (b) dry pasture, hay, alfalfa supplement for 17 days pre-joining	Columbia & Targhee	" "	births/ewe present at lambing	12-14	11-12[b]	medium (?)
8. *Coop (1966)*						
(a) Meadow hay and ryegrass straw (b) best green pasture plus hay plus barley grain	BL X Romney	206	births/ewe lambing	19	10	various
(a) similar to (a) above (b) similar to (b) above	BL X Romney	204 208	"	18	14	various
(a) shorter grass (b) good grass	BL X Corriedale	177 175	"	10	11	various
(a) (b) unspecified	BL X Corriedale	182 182	"	12 6	8 2	poor medium
(a) dry brown pasture and straw (b) saved pasture (bottom green leafy rye grass and clover)	BL X Romney	145	"	10	8	good
(a) (b) unspecified	BL X Romney	180	births/ewe lambing	?	-5 (?)[c] 15 (?)[d]	?
(a) sparse dry grazing (b) saved pasture - rank dry top and bottom of green leaf	BL X Corriedale	206 205	"	9	4[e]	good
(a) overgrazed pasture and pasture hay (b) saved rye grass, Yorkshire fog, white clover	BL X	270	"	12	7[e]	good

Table 18. (continued)

Feeding treatment (a) Control (b) Flushing	Breed	Group size	Type of observation	Total effect (%)	Calculated dynamic effect[a]	Condition flushin
9. *Killeen (1967)*						
(a) matured subterranean clover, annual rye grass or restricted grazing of white clover, paspalum (b) white clover, paspalum	BL X Merino	264	births/ewe lambing	14	4	various
(a) restricted grazing time of same pasture as (b) (b) white clover, paspalum	BL X Merino	120	ovulations/ ewe mating	18	8	various
(a) as for (a) above (b) as for (b) above	BL X Merino	120	ovulations/ ewe mated (all ewes mated)	18	6	various
10. *Gunn, Doney and Russell (1969)*						
(a) pasture and various amounts of supplementary feed	Scottish Blackface	9	ovulations/ ewe present	11	9	medium
(b) as for (a) but greater supplement		9-8		27	18	poor
11. *Fletcher (1971)*						
(a) restricted amount of hay-grain ration	Merino	53-51	ovulations/ ewe present	3	5	good
		49-48		-6	-1	medium
(b) greater amount of hay/grain ration		48-52		-2	3	poor
12. *Cumming (1972)*						
(a) annual ryegrass, subterranean clover pasture	BL X Merino	70	ovulations/ ewe present	12	12	medium
(b) irrigated perennial ryegrass, white clover pasture		64				
13. *Gunn and Doney (1975)*						
(a) various amounts of milled and pelleted dried grass	Scottish Blackface	26 22	ovulations/ ewe present	6	9	medium
		18 14		17	8	poor

a Total effect corrected on the basis of a 10 per cent increase in ovulation and 6 per cent in multiple births for each 4.5 kg increase in mean liveweight at ovulation.
b Flushed for 17 days prior joining.
c Flushed days 3-12 of oestrous cycle.
d Flushed days 13-23 of oestrous cycle.
e Flushed for one oestrous cycle after joining.

conducted using different feeds. The results of Gunn and Doney (1975), however, should be regarded with caution as they related to small groups of ewes and could be subject to considerable experimental error. Some of the experiments involved a specific difference, whereby the flushed group were offered green feed and the control group dry feed. They certainly would have involved a difference in feed quality. The experiments conducted in these circumstances (Tribe and Seebeck, 1962; Coop, 1966 (some); Cumming, 1972) resulted in a similar level of dynamic response to that for all of the experiments conducted using different feeds.

Does feed quality have a greater dynamic effect when ewes are in poorer condition? Comparison within the experiments that had two levels of condition suggest that this may be so. The results presented by Darroch *et al.* (1950), Coop (1966) and Gun *et al.* (1969) each show that there was a greater dynamic response among ewes in poor condition than among those in medium condition. In contrast, the two experiments conducted with different levels of condition but similar feeds (Fletcher, 1971; Gunn and Doney, 1975) showed no difference in the response of ewes in either poor or medium condition.

Consideration of the data shown in Table 18 does not suggest an overall effect of season on the magnitude of the dynamic effect of flushing. However, this conclusion relates to a comparison among experiments that differ in many factors other than season and should be accepted with considerable caution.

In summary, the examination revealed circumstantial evidence that feed quality (type of feed) may partly, or entirely, be responsible for the dynamic effect of flushing, particularly among ewes in poor condition, and that an effect of quality is not obviously related to any particular season of the year. These conclusions emphasise the feasibility, and also probably the likelihood, of differences in feed quality being a factor affecting the levels of ovulation observed among the Field and pen-fed ewes in the present study.

The conclusions from the examination suggest strongly that feed quality, as well as static and dynamic effects of liveweight, should be considered in future examinations of the effect of flushing. It remains to be determined whether the effect of feed quality is only one component of the dynamic effect of flushing or whether the two effects are synonymous. The data examined probably point to it being only a component, as those experiments in which different amounts of the same feed were used still, collectively, exhibited a degree of dynamic response.

(e) Ovulation and season

While the variation in the incidence of multiple ovulation observed between autumn and spring among the High and Low groups was similar to that observed among Koonoona ewes in a previous year, it was less than that reported for medium-wool Merino ewes studied at Melbourne (Radford, 1959). Those ewes were probably maintained in very good condition, for, while liveweight or body condition was not specifically reported, the peak incidence of multiple ovulation recorded was 78 per cent. This might have increased the variation between seasons. However, the greater variation also probably reflects a more clearly defined breeding and non-breeding season among the medium-wool ewes. The phase of the annual cycle of variation in ovulatory activity is probably slightly different too. The Koonoona ewes appear to exhibit both their peak and minimum about six to eight weeks earlier in the year than the medium-wool ewes. It is possible, but I think unlikely, that the difference in both magnitude and phase reflects environmental, not strain, differences.

(f) Liveweight, body condition, body size

The present study and that of Guerra, Thwaites and Edey (1972b) both indicate that of the three parameters liveweight, body condition and body size, the most accurate (or at least equally most accurate) single predictor of ovulation rate is liveweight. Cumming (1977), although not considering body size, also concluded that the prediction of ovulation by liveweight was not improved by the inclusion of a body condition term. As there was a significant correlation between liveweight and body condition in each of these three experiments it would appear that body condition may also be a good indicator or ovulation rate. However, while a significant relationship was detected between body condition and ovulation rate in the present study a similar relationship was not detected by Guerra *et al*. (1972b).

Indeed the predictive value of both body condition and body size is doubtful. This study and that of Guerra *et al*. (1972b) reveal opposite effects. In this study there was a significant correlation between ovulation and body condition index but not body size, while they reported a significant relationship with body size but not body condition index. However, in both experiments, once the variability accountable to liveweight was removed (by partial correlation analysis) there was not a significant relationship with either body condition or body size. The two studies are probably not directly comparable, as Guerra, Thwaites and Edey do not appear to have accounted for possible effects of the treatments imposed in their experiment. The importance of this difference is not clear, but as adjustment for treatment had only a minor effect in the present study - compare analyses with (Table 13), and without, adjustment for treatments (Appendix Table 10) - it is unlikely that the different basis of analysis offers an explanation for the different relationships observed in the two studies.

The absence of a correlation between ovulation rate and body size in the present study is similar to that reported by Ducker and Boyd (1977) for Greyface ewes in Scotland. Further, as the ewes were in moderate to good, and certainly not poor, condition the present observation is consistent with the explanation proposed by Ducker and Boyd to explain the correlation with body size reported by Guerra *et al.* (1972b). Namely, that the Merino ewes observed by Guerra *et al.* were of small body size and low liveweight and they exhibited a low ovulation rate and a high incidence of barrenness, while the Greyface ewes were larger and more prolific and almost all conceived to their first service. They proposed that the Greyface ewes were above, and the Merino ewes below, a certain minimum body size below which body size has a marked effect on ovulation.

(g) Conclusions

1. The study has confirmed the previously observed annual cyclic nature of the occurrence of oestrus, and the incidence of multiple ovulation, among Koonoona ewes maintained at a constant mean liveweight on a hay/grain diet. Almost all the ewes appeared to experience oestrous cycles during March/April, and while only 50-60 per cent naturally did so during September they almost all cycled when stimulated by the

sudden introduction of rams. There was a higher incidence of multiple ovulation during autumn than during spring.

2. This study has extended the previous observations of oestrus and ovulation at sustained liveweight by showing that cyclic variation occurred at a sustained mean liveweight of either 45 kg or 54 kg (compared with 49 kg previously). The difference in sustained liveweight did not significantly affect oestrous behaviour. While there was an overall greater incidence of multiple ovulation at the higher liveweight it is not clear whether or not the amplitude of the annual cyclic variation was greater at the higher, than at the lower, liveweight.

3. When compared at equal liveweight, the oestrous and ovulatory performance of the ewes offered a hay/grain ration was similar irrespective of whether liveweight remained constant or fluctuated on an annual basis: the fluctuation being of similar phase and magnitude to that experienced by ewes grazing in the field.

4. The oestrous and ovulatory performance of the ewes grazing in the field were both significantly different to that of the ewes fed a hay/grain ration in pens. It is not clear why a significantly smaller proportion of the Field ewes, than pen-fed ewes, were still experiencing oestrous cycles during September (i.e. before ram stimulation). As the magnitude of the difference was similar to the between-year variation that may be expected among grazing ewes the difference could reflect a small alteration between the groups in the timing and, or, severity of the anoestrous period.

It is not clear why, even after allowance for small differences in liveweight, there was still apparently a greater incidence of multiple ovulation among the Field ewes during autumn. Although body condition index, and the body components fat, water, lean and protein were measured specifically in anticipation that differences in one or more of these factors would provide the basis for an explanation in this situation, they did not clearly do so. However, the incidence of multiple ovulation was correlated with the estimated mean weight of protein at ovulation. This correlation and other recent reports suggest that it might have been more useful to have measured feed quality.

It is now clear that in some circumstances differences in feed quality can alter ovulatory performance by as much, or more, than the difference observed between the Field and pen-fed groups during autumn without there being a concurrent change in liveweight. A review of the literature of flushing experiments showed that it is also possible that at least part of the so-called dynamic effect of flushing could be due to differences in feed quality. While this evidence did not arise from closely similar conditions to that of this study it seems that differences in feed quality offer a feasible, and indeed the most likely, explanation for the different ovulatory performance of the pen-fed and field grazed ewes during autumn.

5. There were several significantly different performances by the field grazed ewes compared with the pen-fed ewes that should be noted if attempting to apply the performance of pen-fed ewes to a practical grazing situation. While the different pattern of occurrence of oestrus during spring is likely to reduce the reproductive performance of the field grazed ewes, the loss in performance can probably be reduced to an insignificant level by joining for a minimum of eight weeks.

The higher incidence of multiple ovulation during autumn is likely to be of greater practical importance, especially if the increase indicates an effect that is wholly, or partly, attributable to differences in feed quality as concluded in this study. For, if this is correct, feed quality is obviously an additional factor that must be accounted for in predicting the incidence of multiple ovulation among grazing ewes.

6. There was a significant, positive, within-flock linear correlation of ovulation rate with both liveweight and body condition index at ovulation, but not with body size. However, the partial correlation with body condition was insignificant when the variation due to liveweight was removed, and that with liveweight was insignificant when variation due to body condition was removed. Ovulation rate was almost equally well correlated with either liveweight or body condition index in autumn, but was better correlated with body condition than liveweight during spring.

The study did not reveal a significant correlation between ovulation rate and the rate of water turnover. Indeed the outstanding feature of this section of the study was the high degree of inconsistency, between repeated measurements, in the rate of turnover of individual ewes relative to the group average, i.e. the repeatability of an animal having a high or low water turnover was low. In this circumstance it is not surprising that no relationship was detected.

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APPENDICES

Appendix Table 1: Mean unfastened liveweight for each of the treatment groups throughout the experiment.

Date		Treatment group Low	 High	 Variable	 Field
23/12	1971	50.3	50.3	50.3	49.9
5/1	1972	48.6	48.2	48.6	52.5
11/1[a]	"	47.8	48.0	47.9	49.6
19/1	"	45.3	45.1	45.8	49.8
26/1	"	46.5	47.9	47.3	50.4
2/2	"	46.1	48.4	49.7	49.8
8/2	"	46.5	48.6	48.8	48.8
22/2	"	44.9	50.8	46.9	47.4
29/2	"	49.8	54.2	50.4	47.7
7/3	"	48.1	53.4	49.2	48.5
14/3	"	47.9	55.9	48.7	48.0
23/3	"	46.0	54.5	48.0	46.2
5/4[a]	"	49.2	57.4	49.6	47.5
18/4	"	49.8	58.6	49.0	47.2
2/5	"	48.9	58.8	47.5	43.2
16/5[a]	"	49.4	58.8	46.1	44.6
23/5	"	49.5	58.9	46.4	44.2
30/5	"	48.9	58.4	45.9	45.5
6/6	"	49.4	-	45.7	47.2
13/6	"	-	-	48.4	-
14/6	"	-	-	-	48.7
22/6	"	48.9	59.5	47.8	-
23/6	"	-	-	-	53.0
11/7[a]	"	49.8	58.6	49.3	51.8
24/7	"	-	-	-	50.5
26/7	"	46.5	54.6	47.3	-
3/8	"	48.2	54.8	49.0	51.5
17/8	"	48.3	55.3	50.0	54.3
24/8	"	47.5	54.8	50.4	-
4/9[a]	"	49.3	58.0	53.9	57.4
25/9	"	47.6	55.0	51.2	57.0
10/10[a]	"	51.1	58.9	54.6	59.2
19/10	"	51.0	57.9	55.9	60.0
7/11	"	53.1	60.1	58.8	-
14/11	"	-	-	-	62.9
16/11	"	52.2	61.0	58.9	-
23/11	"	52.2	61.2	60.6	62.8
5/12[a]	"	52.6	61.4	60.7	61.0
19/12	"	-	-	-	60.5
21/12	"	53.2	62.4	62.3	-
2/1	1973	-	-	-	59.3
4/1	"	52.2	62.1	61.1	-
11/1	"	54.0	-	62.4	-
16/1	"	-	-	-	57.9
23/1	"	53.5	64.0	61.1	-
1/2	"	53.3	62.6	59.3	-
2/2	"	-	-	-	57.3
12/2	"	-	-	-	54.4
13/2	"	51.7	61.2	57.8	-
20/2[a]	"	51.9	61.6	58.0	55.0
1/3	"	52.5	61.0	56.0	-
2/3	"	-	-	-	56.6
20/3	"	52.3	61.2	55.7	55.6
3/4[a]	"	52.7	61.9	56.8	54.0
12/4	"	52.6	61.3	56.6	54.8

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[a] Values for these dates, although weighed on a fasted basis, have been adjusted upwards using the values shown in Appendix Table 5.

Appendix Table 2. Average monthly rainfall and average daily maximum and minimum temperature - Turretfield Research Centre.

Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Annual
(a) Average monthly rainfall (mm) (average of 76 years)												
18	20	17	37	56	55	57	58	51	42	27	23	459
(b) Average daily maximum temperature (°C) (average of 21 years)												
29.4	29.2	27.0	22.4	17.7	14.8	14.1	15.0	17.2	21.3	24.3	26.8	-
(c) Average daily minimum temperature (°C) (average of 21 years)												
15.4	15.7	13.6	10.6	7.9	5.7	5.3	5.5	6.3	8.4	11.4	13.1	-

Appendix Table 3. Rainfall (mm) recorded at Turretfield Research Centre each half monthly period from May 1971 to April 1973.

Year	1971								1972			
Month	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	March	April
2nd to 16th of month	45.2	39.4	4.3	33.8	37.3	13.2	25.4	17.0	26.4	17.5	0.0	8.4
17th to 1st of next month	24.9	32.8	41.9	40.6	30.5	12.2	17.5	4.6	1.8	5.3	0.0	25.9
Year	1972								1973			
2nd to 16th of month	39.4	0.0	48.3	60.5	22.9	16.0	11.4	0.3	1.0	88.9	2.8	7.9
17th to 1st of next month	6.1	33.0	7.9	34.5	2.3	1.8	0.0	16.5	9.7	0.7	34.3	43.9

Appendix Table 4. Average daily maximum and minimum temperatures (^{o}C) for each half monthly period from May 1971 to April 1973.

	1971								1972			
Month	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	March	April
1st to 15th												
Maximum	16.8	14.8	15.0	14.7	16.3	19.8	23.3	27.2	26.8	31.5	27.0	25.6
Minimum	10.2	8.0	4.5	5.2	5.3	6.6	11.3	13.1	15.0	17.0	12.3	12.1
16th to End												
Maximum	17.4	13.8	14.1	15.0	19.0	21.8	22.2	25.8	30.4	28.7	25.9	22.8
Minimum	6.2	5.8	5.4	6.5	7.6	7.7	9.9	11.5	14.1	14.7	10.1	10.3
	1972								1973			
1st to 15th												
Maximum	23.5	18.3	13.8	13.6	19.9	20.4	23.8	28.7	28.5	27.6	27.5	25.4
Minimum	9.5	3.7	6.5	7.2	6.8	7.7	8.3	12.9	15.3	14.9	14.0	12.8
16th to End												
Maximum	16.4	16.7	14.8	17.6	18.7	24.5	27.4	29.6	35.0	29.6	23.9	19.7
Minimum	6.5	5.0	6.4	6.1	4.0	8.0	12.6	14.7	21.0	17.8	13.7	11.2

Appendix Table 5: Liveweight values (kg) applied to correct measured liveweight for wool weight and fasting.

Time of measurement	Treatment group Low	 High	 Variable	 Field
(a) Wool weight correction (kg)				
0	0.5	0.6	0.5	0.4
1	1.5	1.7	1.4	1.1
2	2.1	2.5	2.1	2.0
3	2.7	3.3	2.8	2.9
4	3.3	4.2	3.6	3.9
5	3.8	4.9	4.2	4.5
6	4.5	5.6	5.0	5.2
7	5.6	6.6	6.1	6.2
8	6.1	7.1	6.8	6.8
(b) Fasting correction (kg)				
0,1,6,7,8	2.1	2.5	2.1	2.1
2,3,4,5	2.1	2.5	2.1	2.6

Appendix Table 6: Proportion of solids in plasma (% by weight) for each group at each Time of sampling.

Treatment group	Time of sampling 0	1	2	3	4	5	6	7	8
Low	8.7	9.9	8.7	8.6	8.5	8.8	9.1	9.2	9.3
High	8.7	9.8	8.7	9.3	8.4	8.3	9.3	9.5	9.1
Variable	8.3	8.1	9.3	8.8	9.2	8.9	9.1	8.8	9.0
Field	9.2	8.4	8.6	9.6	9.3	9.4	9.4	8.9	9.6

Appendix Table 7a: The number and accumulated incidence (%) of ewes detected in oestrus, for each treatment group, during February/March 1972.

Days after rams introduced[a]	Treatment group							
	Low		High		Variable		Field	
	New ewes	Acc %	New ewes	Acc %	New ewes	Acc %	New ewes	Acc %
2	9	16.1	10	18.5	9	16.7	7	12.1
5	12	37.5	9	35.2	9	33.3	11	31.0
7	5	46.4	3	40.7	6	44.4	9	46.6
9	4	53.6	5	50.0	3	50.0	9	62.1
12	7	66.1	5	59.3	5	59.3	6	72.4
14	8	80.4	5	68.5	7	72.2	7	84.5
16	8	94.6	6	79.6	4	79.6	1	86.2
19	0	94.6	1	81.5	1	81.5	2	89.7
21	0	94.6	1	83.3	0	81.5	1	91.4
23	0	94.6	2	87.0	1	83.3	2	94.8
26	0	94.6	1	88.9	2	87.0	2	98.3
28	0	94.6	0	88.9	2	90.7	0	98.3
30	1	96.4	2	92.6	2	94.4	0	98.3
33	1	98.2	2	96.3	1	96.3	0	98.3
35	0	98.2	0	96.3	0	96.3	0	98.3
Total ewes in group	56		54		54		58	

[a] Rams introduced 23.2.72.

Appendix Table 7b: The number and accumulated incidence (%) of ewes detected in oestrus, for each treatment group, during September 1972.

Days after rams introduced[a]	Treatment group							
	Low		High		Variable		Field	
	New ewes	Acc %	New ewes	Acc %	New ewes	Acc %	New ewes	Acc %
2	11	19.6	5	8.9	5	9.3	2	3.4
5	5	28.6	5	17.9	5	18.5	3	8.6
9	7	41.1	10	37.5	4	25.9	2	12.1
12	4	48.2	2	41.1	1	27.8	1	13.8
14	3	53.6	6	51.8	4	35.2	1	15.5
16	0	53.6	3	58.9	2	38.9	3	20.7
19	13	76.8	5	67.9	6	50.0	18	51.7
23	2	80.4	4	75.0	6	61.1	9	67.2
26	5	89.3	4	82.1	4	68.5	8	81.0
28	2	92.9	1	83.9	1	70.4	3	86.2
30	1	94.6	3	89.3	3	75.9	0	86.2
33	1	96.4	1	91.1	3	81.5	1	87.9
35	0	96.4	1	92.9	3	87.0	0	87.9
37	1	98.2	1	94.6	0	87.0	1	89.7
40	0	98.2	1	96.4	2	90.7	0	89.7
42	0	98.2	0	96.4	0	90.7	0	89.7
Total ewes in group	56		54		54		58	

[a] Rams introduced 23.8.72.

Appendix Table 7c: The number and accumulated incidence (%) of ewes detected in oestrus, for each treatment group, during February/March 1973.

Days after rams introduced[a]	Treatment group Low New ewes	 Acc %	 High New ewes	 Acc %	 Variable New ewes	 Acc %	 Field New ewes	 Acc %
3	13	23.2	10	18.5	9	16.7	12	20.7
5	4	30.4	5	27.8	7	29.6	4	27.6
7	10	48.2	6	38.9	9	46.3	9	43.1
10	10	66.1	10	57.4	6	57.4	11	62.1
12	1	67.9	2	61.1	3	63.0	4	69.0
14	3	73.2	1	63.0	5	72.2	4	75.9
16	6	83.9	4	70.4	2	75.9	4	82.8
19	4	91.1	1	72.2	2	79.6	1	84.5
21	0	91.1	3	77.8	2	83.3	0	84.5
24	0	91.1	3	83.3	0	83.3	2	87.9
26	1	92.9	1	85.2	0	83.3	1	89.7
28	0	92.9	1	87.0	0	83.3	1	91.4
32	1	94.6	2	90.7	3	88.9	1	93.1
35	0	94.6	0	90.7	2	92.6	3	98.3
Total ewes in group	56		54		54		58	

[a] Rams introduced 16.2.73.

Appendix Table 8: Mean body size[a], at the beginning and end of the experiment, of those ewes in each treatment group that had complete sets of data.

	Treatment group			
	Low	High	Variable	Field
Mean body size at beginning	36.55	36.33	36.95	36.66
S.E. of mean	0.52	0.58	0.56	0.45
Number of animals	52	50	47	54
Mean body size at end	34.86	38.07	35.41	35.78
S.E. of mean	0.49	0.60	0.62	0.36
Number of animals	52	50	47	54
Significance	*	*	N.S.	N.S.

* $P < 0.05$

N.S. Not significant

a Body size = length (cm) x depth (cm)

$$\times \frac{(\text{width at shoulder (cm)} + \text{width at hips (cm)})}{2 \times 1{,}000}$$

Appendix Table 9: Rankings of ewes selected for a degree of consistency of either high or low water turnover at each of the nine Times of observation.

Ewe No.	Group	No. in group	Ranking at Times T_0 to T_8	Ovulations M72,S72,M73
(a)	*Consistently high*			
5	Low	18	3,5,4,5,14,6,13,16,8	1,1,1
7	"	"	18,8,2,4,3,2,1,1,4	1,0,1
17	"	"	7,1,5,3,4,1,5,4,15	1,1,2
22	High	"	10,1,1,4,6,5,5,6,4	1,2,2
53	Field	"	8,18,18,5,4,18,3,9,2	1,1,1
55	"	"	2,5,12,11,3,3,1,1,3	1,1,1
73	Variable	16	2,11,3,7,3,7,4,3,6	1,0,1
79	"	"	1,1,1,1,1,1,2,6,4	1,2,2
(b)	*Consistently low*			
6	Low	18	12,13,1,15,16,8,12,8,18	2,0,1
8	"	"	17,17,9,13,10,4,11,14,16	1,1,1
13	"	"	14,6,15,7,9,12,18,13,17	2,2,1
14	"	"	13,10,13,18,15,18,14,9,13	1,1,1
20	"	"	15,18,7,9,7,15,16,17,6	2,1,1
23	High	"	18,14,16,12,14,10,15,15,13	1,1,1
38	"	"	17,15,12,3,10,15,10,18,9	1,1,2
78	Variable	16	14,16,14,14,10,15,12,13,14	1,1,1
83	"	"	6,10,10,5,8,10,7,10,2	1,1,2

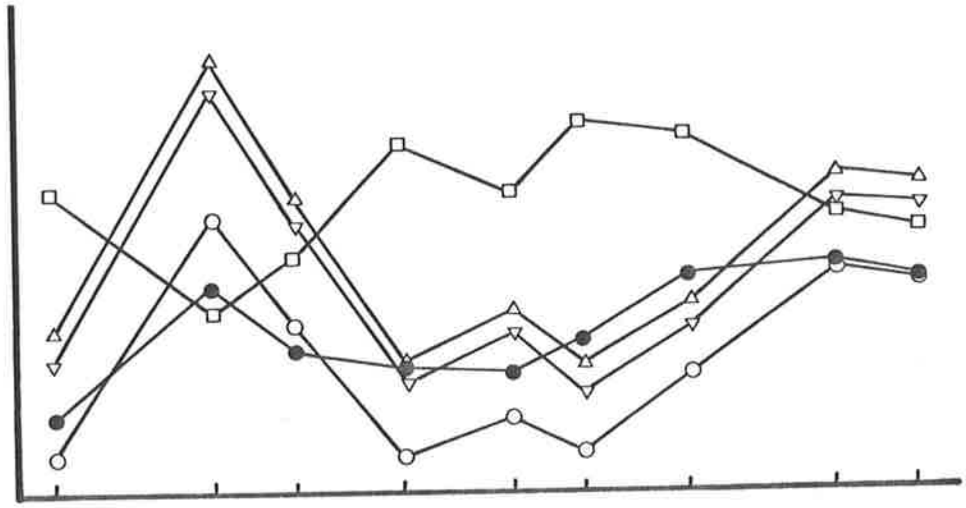
Appendix Table 10. Partial correlation analysis of the relationships between unadjusted[a] values of ovulation rate (OR), liveweight (LW), body size (BS) and body condition index (BC) in March 1972, September 1972 and March 1973.

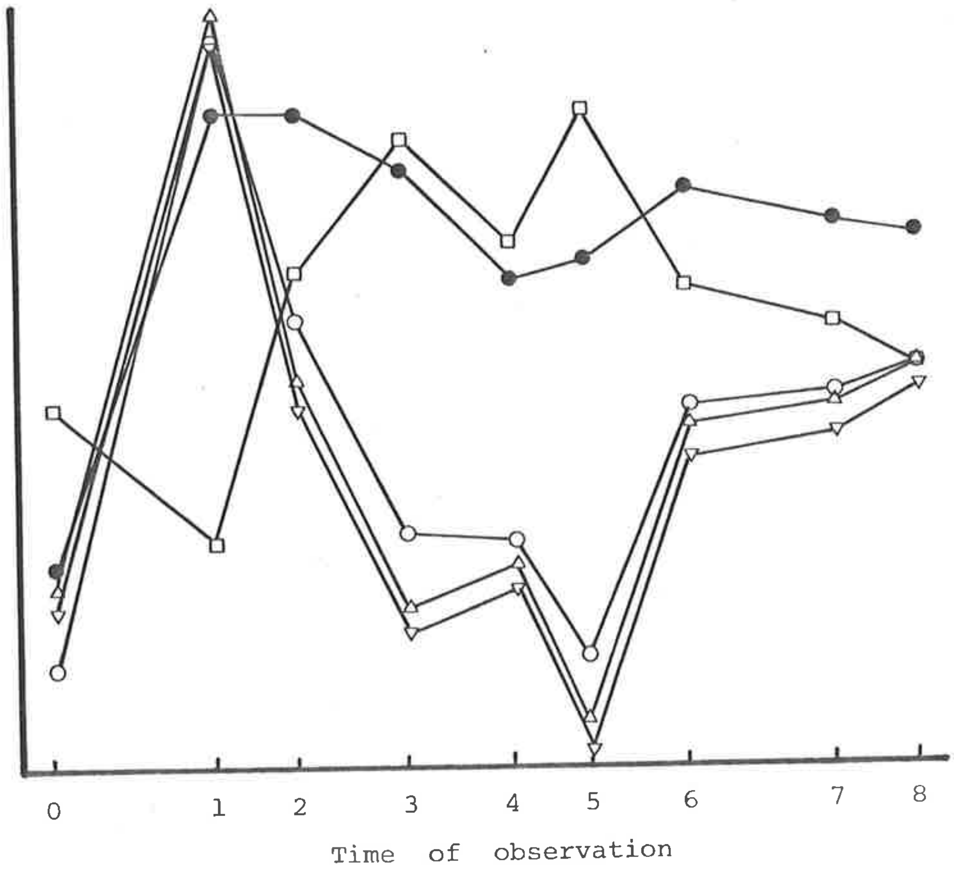
	r value			d.f.	F ratio			Significance		
	M72	S72	M73		M72	S72	M73	M72	S72	M73
(a) Correlations										
OR - LW	0.23	0.18	0.21	200	11.7	6.75	8.87	***	*	**
OR - BS	0.13	0.05	0.13	201	3.56	0.42	3.40	N.S.	N.S.	N.S.
OR - BC	0.22	0.22	0.19	201	9.97	10.1	7.93	**	**	**
LW - BS	0.73	0.68	0.71	201	234.5	173.8	200.0	***	***	***
LW - BC	0.79	0.82	0.82	201	333.2	400.3	427.4	***	***	***
(b) Partial correlations										
OR - BS (LW constant)	0.06	0.11	0.02	200	0.75	2.31	0.11	N.S.	N.S.	N.S.
OR - BC (LW constant)	0.05	0.13	0.05	200	0.57	3.18	0.42	N.S.	N.S.	N.S.
OR - BS (BC constant)	0.10	0.02	0.10	200	1.99	0.06	1.86	N.S.	N.S.	N.S.
OR - LW (BC constant)	0.11	0.004	0.08	200	2.25	0.003	1.32	N.S.	N.S.	N.S.

[a] Unadjusted for differences in treatment means.

Appendix Figure 1. Overlay, for the Low group, of the mean weight of body water (▽), lean (△), protein (○), fat (□) (as depicted in Figures 14, 15, 16, and 17, respectively) and wool-free, fasted, liveweight (●).

Appendix Figure 2. Overlay, for the High group, of the mean weight of body water (▽), lean (△), protein (○), fat (□) (as depicted in Figures 14, 15, 16, and 17, respectively) and wool-free, fasted, liveweight (●).

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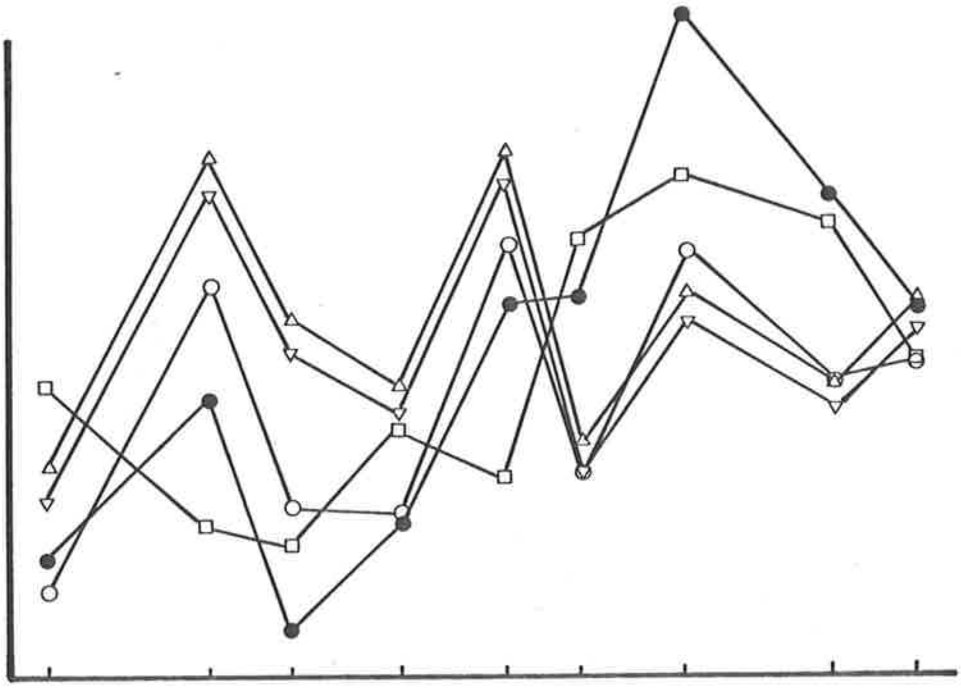
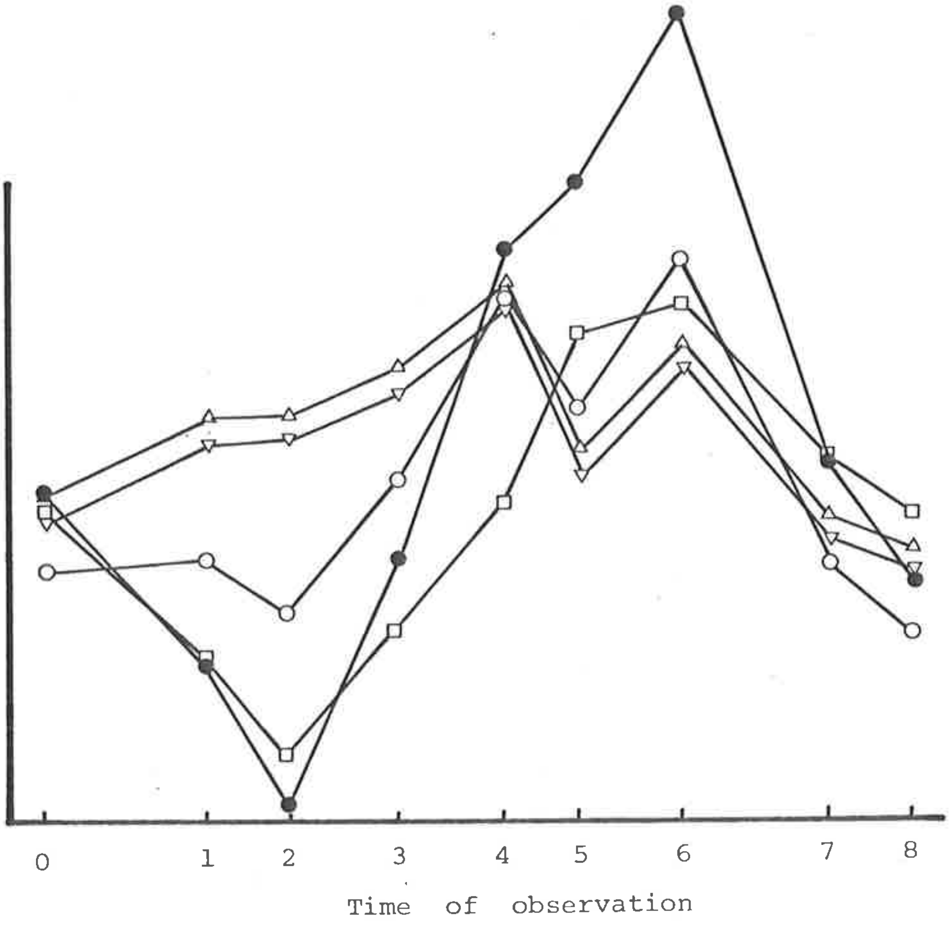
Time of observation

Appendix Figure 3. Overlay, for the Variable group, of the mean weight of body water (▽), lean (△), protein (○), fat (□) (as depicted in Figures 14, 15, 16 and 17, respectively) and wool-free, fasted, liveweight (●).

Appendix Figure 4. Overlay, for the Field group, of the mean weight of body water (▽), lean (△), protein (○), fat (□) (as depicted in Figures 14, 15, 16 and 17, respectively) and wool-free, fasted, liveweight (●).

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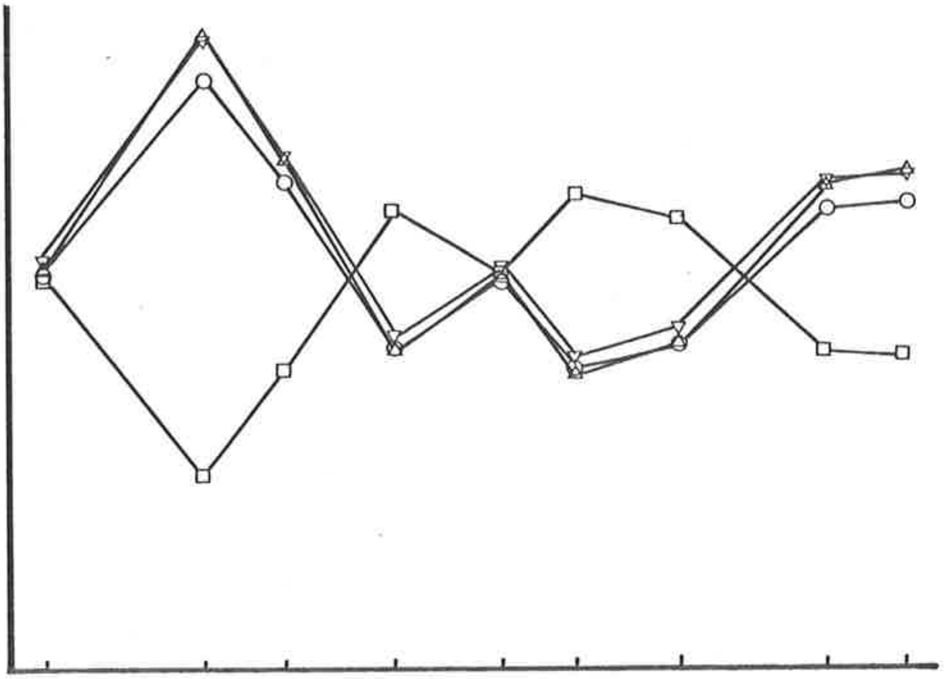
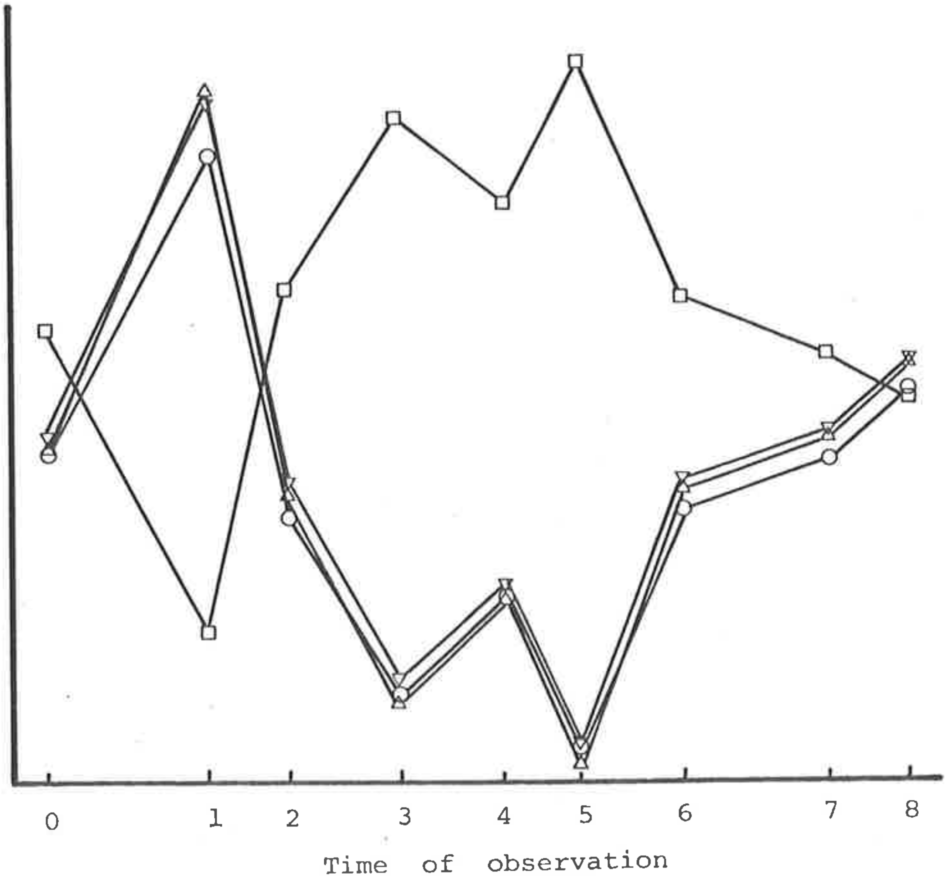
Appendix Figure 5. Overlay, for the Low group, of the mean proportion (% of wool-free, fasted, liveweight) of body water (▽), lean (△), protein (○) and fat (□) (as depicted in Figures 18, 19, 20 and 21, respectively).

Appendix Figure 6. Overlay, for the High group, of the mean proportion (% of wool-free, fasted, liveweight) of body water (▽), lean (△), protein (○) and fat (□) (as depicted in Figures 18, 19, 20 and 21, respectively).

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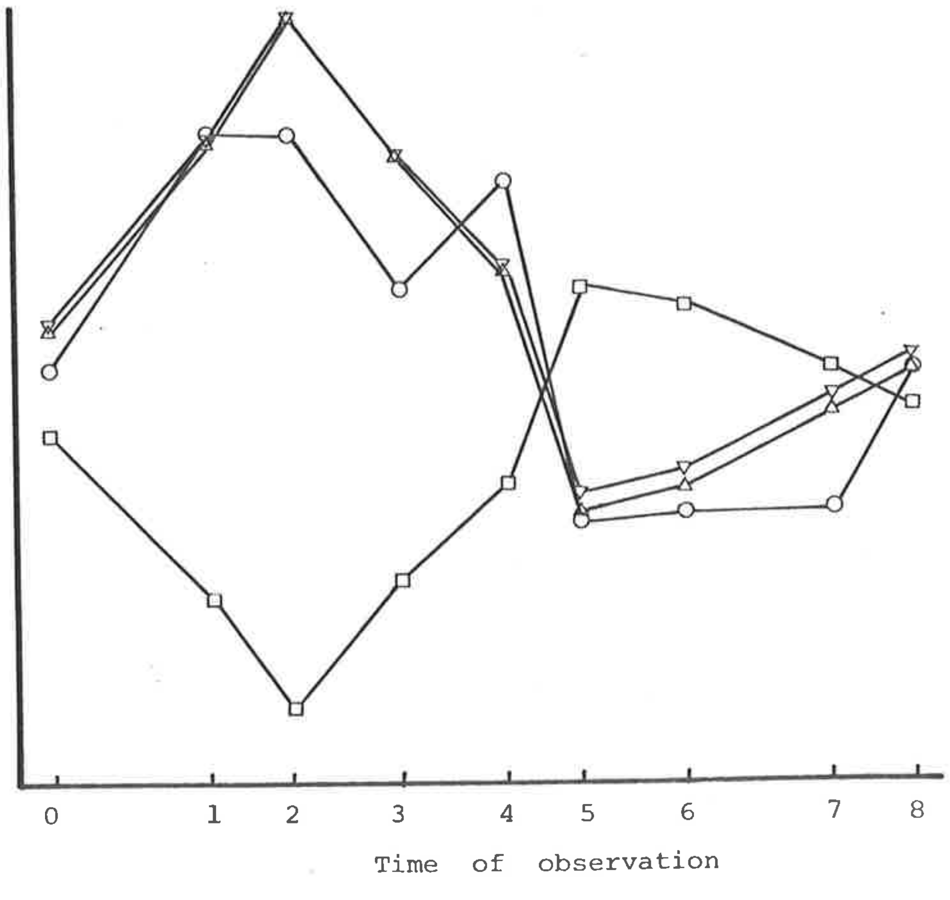
Appendix Figure 7. Overlay, for the Variable group, of the mean proportion (% of wool-free, fasted, liveweight) of body water (▽), lean (△), protein (○) and fat(□)(as depicted in Figures 18, 19, 20 and 21, respectively).

Appendix Figure 8. Overlay, for the Field group, of the mean proportion (% of wool-free, fasted, liveweight) of body water (▽), lean (△), protein (○) and fat (□)(as depicted in Figures 18, 19, 20 and 21, respectively).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