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CURRENT LEVELS OF PERFORMANCE IN THE RUAKURA FERTILITY FLOCK OF ROMNEY SHEEP

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SUMMARY

Data are presented for a flock of mixed-age Romney sheep established in 1948 as a long-term two-way selection experiment comprising animals selected for a high incidence of multiple births (H line), a low incidence of multiple births (L line) and a control (C line).

The average reproductive performance of 2 to 4 year old ewes in the H line has shown a gradual but erratic increase relative to the C line at an average annual rate of round $1\frac{3}{4}$ lambs born and $1\frac{1}{2}$ lambs docked per 100 ewes mated. By contrast, there has been little consistent change in overall reproductive performance in the L line relative to the C line.

Over the period 1967-70, respective reproductive performance averaged for 2- to 4-year-old-ewes in the H, C and L lines was: 0.93, 0.89 and 0.84 for the ratio of ewes lambing per ewe present at lambing; 1.62, 1.22 and 1.13 for the ratio of lambs born per ewe lambing (litter size); and 0.78, 0.78 and 0.88 for the ratio of lambs docked per lamb born. Thus, relative to the C line, litter size made the greatest contribution to the superior overall reproductive performance of the H line, while for the L line, improved lamb survival was compensated for by a small increase in barrenness and a small decrease in litter size.

Data on the growth and wool production of ewe hoggets born over the period 1965-8 are indicative of a small positive correlated response in liveweight at 14 to 16 months of age and a small negative correlated response in lamb and hogget wool production.

FLOCK FORMATION AND BREEDING POLICY

IN 1948 Dr L. R. Wallace initiated at Ruakura a selection experiment for reproductive performance when he formed three closed lines, each of 100 mixed-age ewes, by selecting sheep from a recorded flock of 1,000 Romney ewes (Wallace 1958, 1964). This flock has become known as the Ruakura Fertility Flock. Its three lines have been maintained as separate self-contained breeding units of similar age composition, but managed together as a single flock at all times apart from the mating period when a rotational grazing policy has been followed.

As has been described by Wallace (1958, 1964), the animals forming the base generation of the positive (High)

selection line were chosen on the basis of a high incidence of multiple births for the ewes themselves, or of their dams in the case of the young (two-tooth) ewes. By contrast a Control line was established as a random sample of the original ewes with respect to this characteristic, while a negative selection (Low) line was chosen on the basis of a low incidence of multiple births.

Similar criteria have been used as the basis of selection decisions for entry and retention of animals in their lines in all subsequent years. Thus High (H) and Low (L) line two-tooth ewe replacements were chosen from those whose dams exhibited a high or low incidence of multiple births, respectively, while in the Control (C) line they were chosen on the basis of the visual appearance of the ewes themselves with no consideration of reproduction rate. Once entering their line, all surviving ewes have been retained for at least three lambings at 2, 3 and 4 years of age. After this time, about half of the older H and L ewes were culled on the basis of their frequency of multiple births, while C ewes were culled on their appearance. Six new two-tooth rams were used annually in each of the lines and then discarded. They were chosen on a similar basis to the ewe replacements with the exception that information on the incidence of multiple births for their female grandparents was also taken into consideration for selection decisions in the H and L lines.

With the following exceptions, the flock has been maintained under this breeding and management policy ever since its inception:

(1) From 1959, the number of sires used in each line was reduced to 2 rams passing certain standards with respect to semen characteristics. The collection of sire parentage records was also initiated at this stage and efforts were made to avoid the mating of close relatives (parent-offspring, full and half-sibs).

(2) By 1954 the size of each selection line had increased to 134 ewes giving about 33 ewes (25% of each line) in each of the 2, 3, 4 and 5+ age groups.

(3) In 1965 it was decided to abandon appearance in favour of strict randomness as the criterion for selection in the C line. From that year also, selection decisions in the H and L lines were made on the basis of an index which aimed at adjusting the frequency of multiple births for variations in age and number of lambings. The chosen index (I) is calculated as:

$$I = k (\bar{P} - \bar{X}_k) / 4(k + 3)$$

where, P is the mean incidence of multiple births based on k lambings of the animal's dam and \bar{X}_k is the line mean for ewes with k lambing records. The index was derived as the expected regression of breeding value on the mean performance of the dam, assuming estimates of $\frac{1}{8}$ and $\frac{1}{4}$ for heritability and repeatability, respectively. Index values for maternal grand-dams were halved and added to the dam's value for a combined assessment of breeding value.

RESPONSE TO SELECTION

Unless otherwise stated, the means presented in this paper will be based on only 2-, 3- and 4-year-old animals, since the older animals are a selected sample of those ewes completing 3 consecutive opportunities to lamb. It must be remembered, however, that the H and L ewes entering their lines at 18 months of age are also a selected sample of the total number available. Since in this case the selection decisions will have been made on the basis of the performance of their dams, and because also of the low heritability of reproductive performance and the relatively low selection intensity that is possible on the female side, the positive bias this may cause to estimates of relative genetic merit for the three lines is expected to be small (probably less than 0.02 for the ratio lambs born per ewe mated).

The ratio of the total number of lambs born (dead + alive) per ewe mated (LB/EM) will be used to display the progress that has been achieved in the H and L lines relative to the C, since it is a familiar reproduction parameter that approximates the criteria of selection.

The average lambing percentages at birth (LB/EM) in each year between 1948 and 1970 show a gradual but erratic increase for the H line relative to the C line. The relative divergence for both the H and L lines is presented in Fig. 1 as the difference between the selected lines and the C line for each year between 1948 and 1970. The rates of divergence depicted are expected to be relatively free of the bias resulting from hogget selection since this is likely to have had a fairly similar effect upon reproductive performance in each year.

The linear regression of the difference between the H and C lines on years (1948-70) indicates an annual rate of response of 1.75 lambs born per 100 ewes lambing. Thus a clearcut divergence has been achieved in the H line, there being every indication that the response is continuing over the past few years. By contrast there is a far

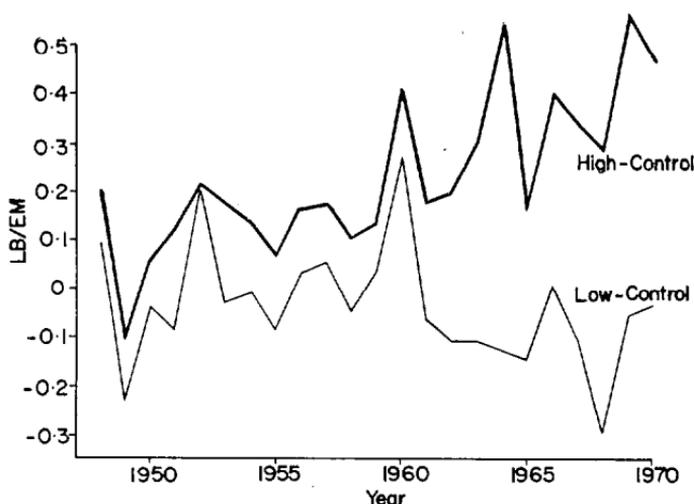


FIG. 1: Annual reproductive performance (lambs born/ewes mated—LB/EM) in the High and Low lines as a deviation from the Control (2- to 4-year-old ewes).

less clearcut divergence between the L and the C lines, although on average the L line has performed at a lower level. Over the past four years for which results are presented, the average performance for the H, C and L lines was 1.49, 1.08 and 0.95 LB/EM, respectively.

In contrast to LB/EM differences between the lines in overall reproductive efficiency as measured by the ratio, lambs docked per ewe mated (LD/EM) are far less impressive. The yearly deviations of the H and L lines from the C line averaged 0.32 and -0.01 for the past four years. However, for this parameter also there remains little doubt that a substantial response has occurred to selection in the H line. For this line, the annual rate of divergence from the C line indicated by the linear regression on years (1948-70) is 1.56 lambs per 100 ewes mated. By contrast no cumulative response is apparent for the L line.

Current levels of some other reproductive parameters will now be examined over the past four-year period in order to investigate more closely some of the biological components of lamb docking percentage for the three lines.

REPRODUCTIVE PERFORMANCE

The ratio, lambs docked per ewe mated and present at lambing (LD/EP), has been used as an overall measure of reproductive performance. It is one which ignores the

pre-lambing ewe death component of docking percentage, but has been chosen because altogether only 24 ewes died between mating and lambing from 1967-70, half of these being 5 years of age or older. For the 2- to 4-year-old ewes pre-lambing ewe deaths averaged 1.3% for the H and L lines and 0.8% for the C line.

The remaining components of reproductive performance have been analysed by classifying ewes according to whether or not they lambed (EL = number of ewes lambing) and all lambs born (LB) according to whether or not they survived to docking (LD = number of lambs docked). This gives rise to the following identity:

$$LD/EP = EL/EP \times LP/EL \times LD/LB$$

The ratios thus reflect the barrenness, litter size and lamb death components of overall reproductive performance.

BARRENNESS ($1 - EL/EP$)

The proportion of ewes lambing of those mated and present at lambing was 0.93, 0.89 and 0.84 for the H, C and L lines, respectively, suggesting that barrenness contributed in some small degree to the line differences in reproductive performance. Thus, for every 100 ewes, 4 fewer were barren in the H line and 5 more barren in the L line relative to the C line. This average deviation of the L line, however, arose almost entirely from a high level of barrenness (0.17) in 1968, which was a below-average year with respect to the proportion of ewes lambing, litter size and lamb survival for all flocks.

Age trends in EL/EP are shown in Fig. 2. While 3-year-old C ewes showed a lower level of barrenness than 2-year-old ewes from the same line, the level rose again at their third and subsequent lambings. The H and L lines exhibited a decreasing level of barrenness to 4 years of age. The net result was an increasing difference with age in the level of barrenness between the H and C lines.

LITTER SIZE (LB/EL)

The average litter size for the H, C and L ewes was 1.62, 1.22 and 1.13 lambs per ewe lambing, respectively, indicating a large positive response to selection in the H line. The age trends shown in Fig. 2 indicate a similar genetic difference between the H and C sheep at each of the first three lambings, the average value being 0.40 lambs per ewe. The difference between the C and L lines, while

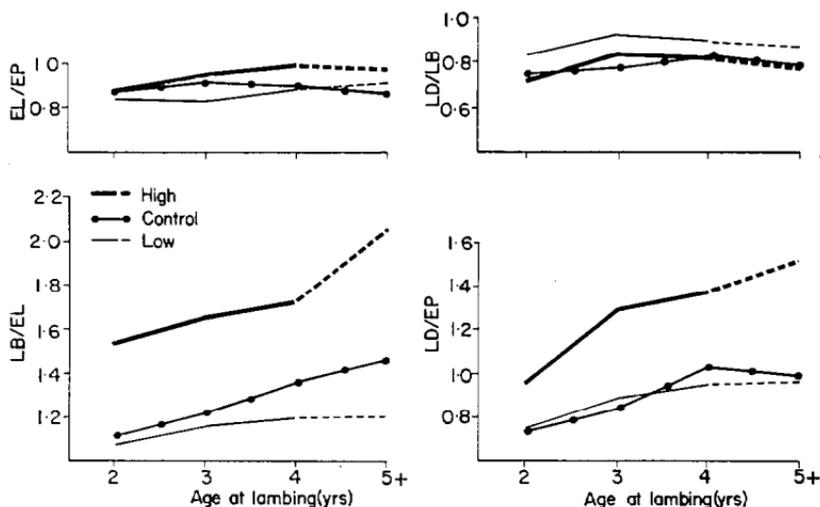


FIG. 2: Age trends in reproductive performance (1967-70). (EP—No. ewes present at lambing; EL—No. ewes lambing; LB—No. lambs born; LD—No. lambs docked.)

averaging 0.09 lambs per ewe over the first three lambings, was about twice as large at the third than at earlier lambings. In both flocks selection of ewes prior to their fourth lambing has increased the deviation of the selected lines from the C line (to 0.59 and 0.26 lambs per ewe for H and L sheep, respectively, *i.e.*, by of the order of 0.18 lambs per ewe from the average values presented above).

LAMB SURVIVAL (LD/LB)

The average survival ratios for the H, C and L lines were 0.78, 0.78 and 0.88 indicating respective lamb death percentages of 22%, 22% and 12%. The age trends are shown in Fig. 2. They indicate a consistent difference of about 0.10 between the L and the remaining lines at all ages and that, within the lines, lamb survival to docking tends to be lower for 2-year-old ewes.

An examination of the causes of the lamb mortality on the basis of field records and post-mortem reports for lambs submitted to the Ruakura Animal Health Laboratory indicated a similar broad pattern of mortality characteristics for this flock and the hill country flock examined by Hight and Jury (1970b), with the exception of a higher incidence of dystokia (about 15% for both singles and multiples) and a higher incidence of physiological starva-

tion (about 10%) for multiple-born lambs. In total the prenatal, dystokia and physiological starvation categories accounted for 74% and 71%, respectively, of all single and multiple-born lamb post-mortems. However, in agreement with Hight and Jury (1970b) the prenatal and starvation categories were relatively more important as a cause of death for multiple-born lambs, while dystokia was more important for the singles. Further examination of the fairly involved interactions that appear to exist between selection line, birth rank, age of dam and birth weight on the causes of lamb mortality must await detailed analysis of further data if a meaningful picture is to be revealed.

DOCKING PERCENTAGE (LD/EP)

The net effect of barrenness, litter size and lamb survival is also shown in Fig. 2. The L and C lines exhibited a similar performance at all ages, their average values being 0.85 and 0.86, respectively. By contrast H ewes were 0.22, 0.44 and 0.35 (average 0.33) lambs per ewe higher than the C ewes at 2, 3 and 4 years of age.

To give an approximate idea of the relative contributions of the three components, the deviations of the H and L lines from the C line have been expressed as a percentage of the C line mean in Table 1. The figures indicate that litter size made by far the greatest contribution to the 39% difference between the H and C lines in docking percentage. For the L line, improved lamb survival compensated for the small changes in barrenness (increase) and litter size (decrease).

TABLE 1: LINE DIFFERENCES AS PERCENTAGE OF CONTROL LINE

<i>Difference</i>	<i>EL/EP</i>	<i>LB/EL</i>	<i>LD/LB</i>	<i>LD/EP</i>
High—Control	+4.8	+32.5	— 0.4	+38.8
Low—Control	—5.1	— 7.4	+12.2	— 0.4

EP—No. ewes present at lambing; EL—No. ewes lambing; LB—No. lambs born; LD—No. lambs docked.

HOGGET CHARACTERS

Records of ewe hogget growth and wool production have been examined up to the time of hogget shearing in December at 16 months of age. Since this is prior to the time when flock replacements have been selected, the data provide an unbiased estimate of relative genetic merit for the three lines and therefore of the correlated responses

that have accrued to selection on reproductive performance. They have been used in preference to data on the adult ewes themselves for the additional reason that they are not subjected to the confounding effects that arise from variations in the reproductive performance of breeding animals.

The hogget data presented are those obtained on animals born from 1965-8 inclusive, *i.e.*, on the same animals whose reproductive performance was earlier examined. The means presented are derived from a least squares analysis which made linear adjustments for the effects of year of birth, age of dam, birth-rearing rank and birth day, additional preliminary analyses having indicated an absence of any significant first order interactions between these main effects. The significant line difference in birth day (H lambs born 4 days earlier than C and 2 days earlier than L animals) was the reason for including birth day as a covariate.

Adjustment of the hogget data for the effects of birth and rearing rank was felt to be justifiable because of its importance as an indicator of a maternally induced environmental handicap on performance in the young animal. That birth rank is also an indication of inherent fecundity because it reflects the number of lambs the animal's dam produced at a given lambing is, therefore, being ignored when such adjustments are undertaken. This genetic component of the effects of type of birth and rearing is likely, however, to have only a small co-variation with the hogget characters examined, especially in relation to the importance of the environmental component. This is supported by the absence of any significant line \times birth-rearing rank interactions.

LIVEWEIGHT

At weaning the average difference in liveweight between the 379 single and the 238 multiple-born lambs was 3.9 kg (8.5 lb) while the difference between the 49 multiples reared singly and the multiples was 2.0 kg (4.5 lb). Twelve months later these differences were 2.2 kg (4.8 lb) and -0.1 kg (-0.2 lb), respectively, indicating that the pre-weaning rearing rank effect on body weight was compensated for during post-weaning growth, while the birth rank effect remained fairly constant at about 2 kg (4.5 lb). This agrees very closely with the results of Ch'ang and Rae (1970) as does the undiminished size of the age of dam effects during hogget growth, although the average differ-

ence between the young (2-year-old) and older dams (-1.2 kg) was only about half as great as their estimate. The regression of liveweight on age was 0.13 kg per day (0.29 lb per day) at weaning and 0.10 kg per day (0.23 lb per day) 12 months later.

The average adjusted liveweights for the three lines at weaning (December), in October, and the following December at the time of shearing, are shown in Table 2. The difference between the H and C lines increased from weaning to a maximum of -1.6 kg (3.4 lb) the following October, but was only -0.9 kg (-1.9 lb) two months later in December. By contrast, L ewe hoggets remained lighter than those from the C line, the difference reaching a maximum of -3.1 kg (-6.7 lb) in December.

TABLE 2: ADJUSTED LINE MEANS FOR HOGGET CHARACTERS

Character	Line		
	High	Control	Low
Weaning weight (kg)	20.8 ± 0.22	21.3 ± 0.25	20.9 ± 0.26
October weight (kg)	43.2 ± 0.36	44.8 ± 0.38	41.7 ± 0.43
December weight (kg)	45.4 ± 0.37	46.3 ± 0.39	43.2 ± 0.43
Lamb fleece weight (kg)	0.88 ± 0.014	0.99 ± 0.014	0.95 ± 0.016
Hogget fleece weight (kg)	3.74 ± 0.041	4.16 ± 0.044	3.81 ± 0.049
Staple length (cm)	15.1 ± 0.13	16.1 ± 0.14	15.9 ± 0.20
Quality number	49.7 ± 0.11	49.2 ± 0.12	48.5 ± 0.14

WOOL PRODUCTION

Age, dam's age, birth-rearing rank and selection line all had significant effects upon both lamb and hogget fleece weights. The adjusted line means are also presented in Table 2.

Both H and L animals clipped less wool than those in the C line, the total wool-producing inferiority of the H animals being 0.5 kg (1.2 lb or 10% of the C line performance). Data obtained on mid-side wool samples for ewe hoggets born over the years 1968-70 have also shown the H line fleeces to be lower yielding by 1.9% , indicating a total clean wool producing inferiority to 16 months of age of about 12% . Relative to the C line, H line fleeces were also shorter in the staple by 1 cm (6%), of slightly higher count on the Bradford scale of quality number, and finer by 1.8μ . L line animals had a similar yield and staple length to those in the C line but a lower count and fibre diameter.

DISCUSSION

Selection experiments are generally undertaken for three main purposes, first, to demonstrate that responses can be obtained from selection pressure for a chosen criterion of performance, and usually also to give some indication of the rate at which these responses accumulate with time. Secondly, they are undertaken to indicate the biological components of the responses achieved and to provide material for an experimental analysis of the physiological processes that have contributed to any genetic changes produced. Thirdly, they can be designed to provide estimates of genetic parameters from an examination of the magnitudes of the direct and correlated responses realized in relation to the selection differentials imposed to achieve them. This permits a reconciliation to be made between the genetic gains predicted from estimates of heritabilities and genetic correlations and those actually realized by selective breeding. Information on all three aspects is required for the selection experiment to make its greatest contribution to knowledge required for the formulation of efficient livestock breeding plans.

This paper has merely given the results of some preliminary analyses that have been undertaken during a study of analytical approaches and methods for handling a more comprehensive analysis of this long-term experiment. The material presented gives some indication of the first two aspects mentioned above. No attempt has yet been made on the third aspect. It is likely to be a fairly involved task because of the problems imposed by overlapping generations, the selection of female replacements, the lack of full pedigree records over the early years of the experiment, variations in rates of inbreeding and the somewhat subjective weighting given in early years to ancestors' fertility records based on different numbers of lambings.

Since the experiment was established in 1948 there has accumulated a considerable amount of knowledge on genetic variation and covariation in the reproductive performance of sheep. This has been recently reviewed by Turner (1969). Of considerable interest from this review is the conclusion that of all the possible components of reproductive performance the most profitable criterion of selection to raise reproduction rate is the high incidence of multiple births. This conclusion is now obvious from the information that is currently available on the heritability and repeatability of lambing rate and its components

—information that certainly was not available when the present experiment was initiated.

There is little doubt that selection has been effective in improving reproductive performance in the H line. For the character LB/EP, linear regression analysis estimated the annual rate of improvement for the H line over the C to be 0.018 lambs per ewe per year, while the average values for the four years investigated suggest an improvement of $0.41/21.5 = 0.019$ lambs per ewe per year.

It is interesting to compare these values with expected rates of improvement under direct selection despite the fact that this requires a large number of assumptions to be made. Assuming values of 1/10 and 1/4 for heritability and repeatability for the generation interval values of 2 and 4 years for males and females, respectively, for the phenotypic standard deviation and the proportions of males and females saved values of 0.7, 4/53 and 33/53, respectively, and that an average of four lambing records on the dam is used to make selection decisions, the expected annual rate of genetic improvement turns out to be 0.021 lambs per ewe per year. The validity or otherwise of these assumptions will be tested when more detailed analyses are attempted in the future. Turner (1968) reported that the difference in this fertility parameter, between two groups of Merino sheep (2- to 4-year-olds) selected for a high and low incidence of multiple births, increased by 0.023 lambs per ewe per year between 1958 and 1967, although more recent results suggest an even greater rate of response for her experiment (H. N. Turner, pers. comm.). For the present experiment also, Fig. 1 is slightly suggestive that the annual rate of improvement over the past ten years may have been somewhat higher than the average rates indicated above.

Little change seems to have resulted from the selection practised in the L line of this experiment. This is hardly surprising in view of the low heritability and the low selection differentials possible for a low incidence of multiple births in a flock where the average litter size has been only about 1.2 lambs.

The overall levels of reproductive performance presented for the C line are not particularly impressive, although there does not appear to be any marked time trend for these sheep over the course of the experiment. It should be remembered, however, that the means presented in this paper refer mainly to 2- to 4-year-old ewes which have been stocked fairly intensively on an area subject to summer dry periods and growing pastures of no special

TABLE 3: COMPARISON OF REPRODUCTIVE PERFORMANCE IN TWO ROMNEY FLOCKS (2- to 4-year-olds)

<i>Flock</i>	<i>EL/EP</i>	<i>LB/EL</i>	<i>LD/LB</i>	<i>LW/LB</i>	<i>LD/EP</i>	<i>LW/EP</i>
Control Line	0.89	1.25	0.79	0.78	0.86	0.85
Hill Country	0.86	1.08*	—	0.77	—	0.75

EP—No. ewes present at lambing; EL—No. ewes lambing; LB—No. lambs born; LD—No. lambs docked; LW—No. lambs weaned.

*Calculated as the proportion of ewes lambing multiples + 1.

merit. The absolute levels of reproductive performance reported for the C sheep may be compared with the means reported for hill country Romney ewes of comparable age extracted from the recently published data of Hight and Jury (1970a). The comparison is made in Table 3, the means for the hill country flock being based on the RCR and RER flocks for 2- to 4-year-old ewes only. It highlights the ratio LB/EL as the main component responsible for the difference in overall reproductive performance between the two flocks.

The finding of little overall difference in lamb death rates to docking or weaning between the H and C lines is intriguing, and is one requiring urgent verification for the larger body of data available from this experiment, particularly as Wallace (1964) earlier reported a small difference in favour of the C sheep and as most other workers have usually reported that death rates to weaning for multiple born lambs are higher than for single born lambs (Turner, 1969; Hight and Jury, 1970b). A more detailed and comprehensive study taking into consideration the effects of birth weight and age at death, in addition to birth rank and age of dam, will hopefully shed greater light on the reasons for the observed line differences. Although the correlated responses in hogget growth (and therefore probably also for inherent adult body size as well) do not appear particularly marked, the results presented by Hight and Jury (1970b) and other workers indicate that a small difference in birth weight could have a large effect on lamb survival and particularly upon the differential survival values of singles and multiples born to dams of different age.

Although the line means presented for the hogget characters are not subject to any bias arising from the selection of flock replacements, their interpretation as correlated responses to selection on reproductive perform-

ance must be treated with caution. This is because in early years of the experiment C animals were selected on visual appearance, it being likely that this practice resulted in positive selection differentials for bodyweight. Consequently until this possibility is investigated it is preferable to use the relative performance of the H and L lines as a guide to the correlated responses in hogget characters. On this basis, only small correlated responses are indicated by the results presented in Table 2. The difference between the H and L lines as a percentage of the L line level was zero, +4%, +5% and -3% for weaning weight, October weight, December weight and total wool production, respectively.

The effect of inbreeding is a further avenue deserving examination for this experiment in view of the relatively small effective population size for each of the lines. The results of Lax and Brown (1968) for Merino sheep point to quite severe effects of inbreeding upon LB/EP and lamb survival.

These are examples of some of the avenues that require investigation at the present stage of this very valuable experiment. Other avenues that are planned for investigation relate to the efficiencies of meat production for sheep of varying genetic reproductive ability and the interactions of these characters with the intensity of stocking.

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Dr L. R. Wallace's contribution in designing and running this experiment up to 1965 is especially acknowledged as are the efforts of the large number of field and recording staff who have been involved with this long-term experiment. In particular, E. H. Cox, J. P. Muller, C. M. Simmonds and Dr A. R. Quartermain have been largely responsible for conducting the experiment over the period covered by this report.

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