A genetic basis for physiological changes in response to stress
by Onkar Singh Phalora

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Genetics
Montana State University
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Abstract:
This study involves 96 two-year-old ewes, and 60 lambs produced by them. Two different breeds whose origins have been tentatively traced to different areas of the world were used. These were Rambouillet and Hampshire. Ten of each breed were used in 1962, 20 in 1963 and 18 in 1964.

The ewes were kept together in one flock for 30 days prior to the introduction of rams. The breeds were separated and the rams run with their respective breeds for the next 20 days. During the next 90 days half of the ewes from each breed received feed at the level recommended by the Rational Research Council. The rest received two-thirds of that amount.

Half of the ewes of each breed on a given feed level were then shifted to the other feed level for the remainder of the gestation period. All ewes on a given feed regimen were run together regardless of breed.

The following measurements were made on the ewes at the start of the feeding program, at change-over, and one day after parturition: hemoglobin, hematocrit, hematocrit-hemoglobin ratio, total plasma protein, albumin-globulin ratio, total WBC count, polymorphs, lymphocytes, thyroid level, and weight. The same measurements, plus oxygen consumption were taken on the lambs (one lamb per ewe).

The Hampshire ewes showed higher levels (statistically significant) in total plasma protein, total WBC count, lymphocytes and hemoglobin, at the beginning. They were also higher, (but not statistically significant) in hematocrit, and body weight. They were lower (but not statistically significant) in albumin-globulin ratio, hematocrit-hemoglobin ratio, and in polymorphs.

During parturition the Hampshires sustained a, greater decrease in total plasma protein, hemoglobin, and hematocrit; a lesser decrease in lymphocytes, albumin-globulin ratio, and weight; a greater increase in hematocrit-hemoglobin ratio; and a lesser increase in polymorphs and total WBC count.

The differences between the two breeds had actually been reversed in total WBC count and hematocrit; but there were no statistically significant differences at parturition.

The Hampshires gave birth to lambs with higher hematocrit, hemoglobin, hematocrit-hemoglobin ratio, albumin-globulin ratio and weight, but lower in total plasma protein, total WBC count and polymorphs.

The Hampshires showed higher lamb to ewe ratios in polymorphs, hematocrit, hematocrit-hemoglobin ratio and albumin-globulin ratio; but lower lamb to ewe ratios in total plasma, protein, total WBC count, lymphocytes and hemoglobin.

The lambs were actually higher than the ewes in polymorphs, hemoglobin and hematocrit for both breeds.

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ABSTRACT

This study involves 96 two-year-old ewes, and 60 lambs produced by them. Two different breeds whose origins have been tentatively traced to different areas of the world were used. These were Rambouillet and Hampshire. Ten of each breed were used in 1962, 20 in 1963 and 18 in 1964. The ewes were kept together in one flock for 30 days prior to the introduction of rams. The breeds were separated and the rams run with their respective breeds for the next 20 days. During the next 90 days half of the ewes from each breed received feed at the level recommended by the National Research Council. The rest received two-thirds of that amount. Half of the ewes of each breed on a given feed level were then shifted to the other feed level for the remainder of the gestation period. All ewes on a given feed regimen were run together regardless of breed.

The following measurements were made on the ewes at the start of the feeding program, at change-over, and one day after parturition: hemoglobin, hematocrit, hematocrit-hemoglobin ratio, total plasma protein, albumin-globulin ratio, total WBC count, polymorphs, lymphocytes, thyroid level, and weight. The same measurements, plus oxygen consumption were taken on the lambs (one lamb per ewe).

The Hampshire ewes showed higher levels (statistically significant) in total plasma protein, total WBC count, lymphocytes and hemoglobin, at the beginning. They were also higher, (but not statistically significant) in hematocrit, and body weight. They were lower (but not statistically significant) in albumin-globulin ratio, hematocrit-hemoglobin ratio, and in polymorphs.

During parturition the Hampshires sustained a greater decrease in total plasma protein, hemoglobin, and hematocrit; a lesser decrease in lymphocytes, albumin-globulin ratio, and weight; a greater increase in hematocrit-hemoglobin ratio; and a lesser increase in polymorphs and total WBC count.

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The lambs were actually higher than the ewes in polymorphs, hemoglobin and hematocrit for both breeds.

INTRODUCTION

Although many investigators have reported work on genetic differences in the level of various biological agents concerned with physiological functions in the mammal, there is very little information concerning the influence of environmental factors on the magnitude of those differences. Any such differences in genotypic response to environmental change could be taken as evidence of genetic differences which have accumulated at times when the groups being compared lived under environmental conditions which differed more widely than those under which they currently live. One group might, for example, have been evolved in an area where feed was barely adequate for the maintenance of life. Under such circumstances the process of reproduction would become a source of stress and would require an increase in efficiency of use of nutrients. Genes which would permit the organism to make a shift in the level of chemical agents to meet such a stress would be expected to accumulate in such an organism. If then, at some later stage in evolution, that organism migrated to an area of adequate feed, those genes would no longer be of importance, in fact their presence would not be evident in the grosser aspects of growth and reproduction. However, such genes might remain at gradually decreasing frequencies for many generations. Their presence would become recognizable at times of relative stress. Furthermore, their presence, although not evident in the grosser aspects of growth and reproduction, might be reflected in changes in the level of various biological agents.

The fact that the phenomenon of genetic differences which are expressed only under particular environmental conditions is commonly observed under programs of artificial selection lends strength to the supposition that it would also occur under natural selection. However, under natural selection the process of accumulation and dissipation of such gene pools would be slower.

Two breeds of sheep whose recent history indicates that at least part of their evolution occurred under fairly divergent environmental conditions were chosen as sources of genetic variation. The two breeds were then subjected to four different patterns of feed restriction, and to the stress of pregnancy in an effort to obtain more information concerning their body functions.

REVIEW OF LITERATURE

A. VARIATION IN HEMOGLOBIN AND HEMATOCRIT LEVEL

1. Effect of Protein Intake

In general, protein intake appears to have little effect upon hemoglobin and hematocrit levels. Weimer and Nishihara (1957) maintained one group of adult rats on a protein-free diet, and completely withheld food from another group until the animals had lost 25% of their original weight. There was no change in hemoglobin nor in hematocrit levels on the protein-free diet, and there was an increase when food was completely withheld. The same workers (1959b), using a protein-free diet, and a diet inadequate in protein (2% casein) until 25% weight loss occurred, showed that during depletion there was no change in either hemoglobin or in hematocrit values in the group of rats which was on a protein-free diet, but that there was a decrease in these characteristics in the group which was on an inadequate protein diet. During repletion there was a decrease in hemoglobin and hematocrit level in the groups on both types of feeding, although the decrease was greater in the group which was on the protein-free diet. Peo et al, (1957) tried the protein depletion-repletion technique with baby pigs. They depleted the baby pigs on a protein-free diet for five weeks; the repletion was done using various levels of protein. Values of hemoglobin and hematocrit were higher during depletion than with any of the levels of protein diet during repletion. They attributed the changes in hemoglobin and hematocrit level to changes in plasma volume. This plasma volume change has also been mentioned by Weimer and Nishihara (1959a) and Allison (1955).

The results of several studies indicate that 50% reduction of dietary protein does not appreciably affect the level of hemoglobin and hematocrit in domestic animals. Howes et al. (1957) fed 100% and 50% of the NRC recommended protein allowance to 12 Hereford and 12 Brahman yearling heifers and were able to demonstrate no difference in hemoglobin and hematocrit level due to food intake. Howes et al. (1963) gave the above mentioned feed levels to 24 Herefords and 24 Brahmans. They pointed out that there was no significant difference in hemoglobin and hematocrit level due to feed intake. Bedrak et al. (1957) fed 100, 77, 56 and 46% of the NRC recommended level of protein (all rations contained equal amounts of energy, vitamins and minerals) to Hereford heifers for 140 days and found that the average values of hemoglobin were 11.71, 12.64, 11.22 and 10.72% and that the levels of hematocrit were also highest at 77% of the NRC recommended protein level. The values on 56% protein level were close to the values on 100% protein level. This result is in agreement with the findings of Howes et al. (1957) and Howes et al. (1963), as mentioned above. These workers did not find any significant difference in hemoglobin and hematocrit levels between 50% and 100% levels of protein. Bedrak et al. (1956) fed rations containing the following levels of protein with equivalent amounts of energy, vitamins and minerals to four groups of yearling heifers: Group I (control) was fed at the NRC recommended level of protein, Group II 64%, Group III 31%, and Group IV 10% of the control level. After 140 days on the above rations, hemoglobin values were 10.82, 10.70, 9.31 and 7.58% for Groups I through IV; and hematocrit values were

42.19, 41.80, 37.05 and 28.78% for Groups I through IV. There was very little difference in hemoglobin and hematocrit level between the 100% and 64% levels. The difference was marked on protein levels of 31% and 10%; but it should be noted that animals on these levels of protein ate less.

2. Genetic Effects

Genetic differences in hemoglobin and hematocrit levels have been demonstrated in several mammals: in sheep by Loggins et al. (1960) who showed that both levels were higher in Florida Native than in either Hampshire or Rambouillet ewes; in cattle by Price et al. (1957), Price (1958), McDonald et al. (1956), Alexander et al. (1959), Blincoe and Brody (1951) and Evans (1963) among breeds of cattle, including Brahman as well as European breeds; in horses by Stankiewiez et al. (1960) and Macleod (1946) between non-thoroughbred and thoroughbred. However, no genetic difference was evident in work by Long et al. (1952), Brody et al. (1949), Korsbang (1962) or Schilling and Salobir (1958), all using various breeds of cattle, and Ullrey et al. (1965b) among breeds of sheep.

3. Effect of Temperature

Environmental temperature does not change the hemoglobin and hematocrit level in humans, according to the findings of Bazett et al. (1940). The same is true of cattle according to Brody et al. (1949) and Blincoe and Brody (1951).

4. Effect of Pregnancy

Ullrey et al. (1965b), working with Hampshire, Shropshire and Suffolk breeds of sheep, found that hemoglobin concentration and hematocrit values

were higher in pregnancy, except towards the end, compared to non-pregnant animals 12 months of age. At parturition there was a slight increase, followed by a decrease at 14 days after parturition. Reynold (1953) showed that in Guernsey cows there is no change in hematocrit reading at various stages of the pregnancy period. Stankiewiez et al. (1960) reported that blood count is not changed by pregnancy in thoroughbred and Fjord horses either.

B. LEUCOCYTE COUNTS

Leucocyte count has been studied under three categories: (a) total, (b) lymphocytes and (c) neutrophils.

1. Effect of Diet

Grunsell (1955) reported that a diet providing half maintenance has no effect on the blood picture in Scottish Hill sheep. Bedrak et al. (1957) fed 100, 77, 56 and 46% of the NRC recommended level of protein to Hereford heifers and found that WBC count was 7,880, 8,096, 6,632 and 8,112 respectively. There was no mention of statistical significance. Keys et al. (1950) mentioned conflicting reports on human WBC count, but generally in semi-starvation there is a mild leucopenia with a relative lymphocytosis.

2. Effect of Age

Comparisons of total WBC count in young and adults have been made by: Josland (1933), Reda and Hathout (1957) and Ullrey et al. (1965a) in sheep; and by Stankiewiez et al. (1960), Hansen et al. (1950) and Todd et al. (1951) in horses. The results are conflicting. The reason for conflict appears to be that the studies have not been done on animals of the same

age by various workers. Of course, species and breed differences cannot be ignored as a possible cause of differences in results. However, the results of the study by Ullrey et al. (1965a) in Hampshire, Shropshire and Suffolk breeds of sheep seem to be quite clear and show that the total leucocyte count rose until 12 hours after birth in the neonate. After a short decline at 48 hours, the count increased, reaching a peak at three months of age. According to the results of Gardiner et al. (1953), Ullrey et al. (1965a), and Reda and Hathout (1957), the most striking change was the shift from an excess of neutrophils in the young to an excess of lymphocytes in older animals.

3. Genetic Effects

Genetic differences in total WBC count have been shown by Alexander et al. (1959) between Angus males and Hereford males. Within the Hereford breed both Lionheart and David male calves had cell counts higher than those of Prince male calves. Genetic differences in total WBC count have also been reported by Milicevic (1960) among Duroc, Hampshire, Poland China and Landrace breeds of pigs before and after mechanical stress, and by Tutikawa et al. (1958) between SM/Rr and dba/MS strains of mice after X-irradiation.

Genetic differences in these cellular fractions have also been shown. Price (1958) reported that Hereford females exhibited higher average lymphocyte counts and lower average neutrophil counts than Angus females. Differences in neutrophil and lymphocyte levels have also been reported by Stankiewiez et al. (1960) between Fjord and thoroughbred horses.

The existence of genetic differences in total WBC count, lymphocyte count and neutrophil count have not been evident in all studies, however. Ullrey et al. (1965a) using Hampshire, Shropshire and Suffolk sheep, Todd (1952) using Hampshire and Southdown sheep and Milicevic (1960) using Landrace, Hampshire, Poland China and Duroc pigs, found no differences.

4. Effect of Pregnancy

Luke (1953a), Kerr et al. (1951) and Ullrey et al. (1965a) all reported an increase in neutrophils and a decrease in lymphocytes toward the end of pregnancy in swine, cattle and sheep, respectively. Luke also showed that a well-marked lymphopenia and neutrophilia is usually apparent during the 6 to 30 hour period prior to parturition. Kerr et al. (1956) found that the differential WBC count at intervals from shortly before calving through the period 24-48 hours after parturition showed lymphopenia and neutrophilia, with the peak reaction about 5-9 hours after delivery. They found that this was also the period of peak level in the cellular reaction after injection of cortisone into non-pregnant animals. Luke (1953b) injected ACTH and adrenal cortex extract into normal non-pregnant pigs and demonstrated a marked lymphopenia and neutrophilia closely resembling that following parturition, and he concluded that the extract of the adrenal cortex is released near and during parturition. Straub (1959) suggested that this picture is one of mild and moderate stress.

C. THYROID ACTIVITY

1. Effect of Feed Level

Observations by Hatch et al. (1963) indicate that there is no difference in thyroid secretion rate in sheep fed 66.6% and those fed 100% of

the NRC recommended feed level. Howes et al. (1962) found that a reduction of 50% in dietary protein intake reduced the amount of I^{131} retained by the gland of Hereford and Brahman cattle.

2. Effect of Pregnancy

Thyroid secretion rate is not significantly affected by pregnancy in sheep, cattle, goats or rats according to reports by Robertson and Falconer (1961), Henneman et al. (1955), Soliman et al. (1963), Flamboe and Reineke (1957), Monroe and Turner (1948) and Dubowitz et al. (1962). However, Danowski et al. (1950) and Grosblat (1963) pointed out that PBI was higher in pregnant women.

3. Effect of Lactation

Thyroid secretion rate is not significantly affected by lactation in dairy cattle except for a slight increase in the beginning according to Soliman et al. (1963), Mixner et al. (1962) and Swanson et al. (1957). Monroe and Turner (1948) reported that lactation has no effect on thyroid secretion rate in rats. The effect of lactation is apparently influenced by other factors, however, according to Flamboe and Reineke (1957) who reported no difference in thyroid activity in lactating and non-lactating goats in May, but in July the thyroid secretion of the non-lactating was higher.

4. Genetic Effects

Several workers have presented evidence of genetic control of thyroid secretion rate. These include Henneman et al. (1955) (sheep); Hatch et al. (1963), Hentges et al. (1962), Mixner et al. (1962), Howes et al. (1962)

and Long et al. (1951) (cattle); Lyon (1956) (mice); Romack et al. (1964) (swine); and Stahl et al. (1962) (chickens).

The fact that genetic differences are not always evident was shown by Eleftheriou and Zarrow (1961), who reported no significant difference in thyroid activity in two subspecies of deer mice at birth; however, at 70 days of age there was a significant difference between the two. A similar situation was noted by Henneman et al. (1955) who demonstrated a genetic difference in thyroid activity between Hampshire and Shropshire sheep, significant at the 1% level in January, at the 5% level in December and at the 10% level in September; while in July the average for the two breeds was very similar. This is a clear example of genetic-environmental interaction. To say that a particular characteristic is genetically controlled or is not genetically controlled, without defining the environments, is not always justified. Thus the following findings cannot go unqualified in spite of the fact that they all showed no genetic difference in the thyroid secretion rate: Lewis and Ralston (1953), Sorensen (1957) and Pipes et al. (1963) among breeds of cattle; Sorensen and Moustgaard (1957) between breeds of pigs; Okamoto et al. (1961) between breeds of chickens; and Matsuo (1961) among various strains of mice.

5. Effect of Temperature

Another source of nongenetic influence on the thyroid secretion rate is the environmental temperature. This can be in the form of seasonal or experimentally controlled temperature.

The thyroid level has been shown to be lower in summer than in winter by Griffin et al. (1962) and Henneman et al. (1955) in sheep (it was lower in July than in any other month). A similar situation has been demonstrated in cattle by Lodge et al. (1957) and Mixner et al. (1962); in goats by Flamboe and Reineke (1959); and by Stahl and Turner (1961) and Okamoto et al. (1961) in chickens.

The effect of the temperature of the ambient air has been studied by Hoersch et al. (1960) and Brooks et al. (1962) on sheep. The results show that thyroid secretion rate becomes lower as the temperature increases. Similar observations have been made by Johnson (1958) and Thompson et al. (1963) in cattle. These results are consistent with the studies of seasonal effect described above.

6. Effect of Light

In sheep, Hoersch et al. (1960) have demonstrated that by increasing the illumination from 4 hours to 12 hours, thyroid activity was progressively depressed, but with added light above 12 hours, the secretion rate steadily rose. The highest values were obtained under continuous light.

D. BLOOD PLASMA PROTEINS

1. Effect of Level of Protein Intake

Weimer and Nishihara (1957, 1959a & 1959b), Weimer et al. (1959) and Weimer et al. (1959a, 1959b) depleted rats by complete starvation, protein-free diets and protein limited diets until some given percentage of their weight was lost, and then repleted them with various levels of protein in their diets. During depletion there was little or no change in total serum

protein, but during repletion there was almost invariably a decrease. These changes were comparable to the changes in level of hemoglobin.

Weimer and Godfrey (1964) showed that the quantitative changes in the serum protein fractions under various types of nutritional stress were different and specific.

Steinbock and Tarver (1954), Jeffay and Winzler (1958) and Soloman (1952) reported that the turnover rate of plasma protein fractions depends upon the level of dietary protein, albumin showing a longer life and slower replacement rate on low protein diet. Jeffay and Winzler (1958) showed that the turnover rate of globulin did not seem to be as much affected by the level of dietary protein.

In baby pigs, Peo et al. (1957) noted similar changes, in total plasma protein during depletion-repletion, to those shown by Weimer and Nishihara, but they felt the changes could be explained by the effect of concurrent changes in plasma volume. Similar changes in plasma volume have been described by Allison (1955) and by Weimer and Nishihara (1959a).

Howes et al. (1957) could not detect any difference in total serum protein between a diet providing 100% and one providing 50% of the NRC recommended protein allowance in Herefords and Brahmans. Bedrak et al. (1956) fed 100, 64, 31 and 10% of the NRC recommended protein allowance for 140 days to groups of 5 yearling heifers averaging 480 pounds, and showed that total plasma protein was 6.68, 6.90, 6.24 and 5.76%. Bedrak et al. (1957) using 100, 77, 56 and 46% of recommended protein allowance for 140 days on groups of 5 two-year-old heifers averaging 666 pounds found

7.72, 7.98, 7.10 and 7.14% total plasma protein respectively. It can be seen that there is no decrease of protein in the plasma associated with decreases in protein intake of less than 40%.

2. Genetic Effects

Condy and Carr (1961) observed an interesting example of genetic control on total serum protein, and albumin and globulin fractions in Afrikander, Mashona and Ngami cattle. Their results indicate that there is a significant breed difference in total serum protein. Mashona, with the higher total protein, has the same concentration of albumin as the Afrikander, thus indicating that different genes control albumin and globulin formation. Genetic control in total serum protein has also been shown by Blincoe and Brody (1951) and Price (1958) between breeds of cattle, and by Kariks and Hipsley (1961) in New Guinean and Australian women.

Although a genetic basis for differences in plasma protein is clearly evident, it is not always apparent. No breed differences were found in the work reported by Howes et al. (1957) between Hereford and Brahman cattle, Ullrey et al. (1964) among Hampshire, Shropshire and Suffolk sheep, or Stankiewiez et al. (1960) between thoroughbred and Fjord horses.

3. Effect of Temperature

Blincoe and Brody (1949, 1951) reported that there is no effect of atmospheric temperature on the level of total plasma protein among Jersey, Holstein and Indian evolved (Brahman) cows.

4. Effect of Pregnancy

The report of Ullrey et al. (1964) on three breeds of sheep (Hampshire, Shropshire and Suffolk) shows that there are fluctuations in total serum

protein during pregnancy. There was a decrease toward the end and at 14 days after parturition. However, total serum protein remain unchanged throughout gestation in humans according to Leyssac (1960). Stankiewiez et al. (1960) report similar results with thoroughbred and Fjord horses.

Peterson et al. (1961) demonstrated that there is a decrease in albumin and an increase in the fractions of globulin, other than beta, in pregnant hamsters. Ullrey et al. (1964) found lower levels of plasma protein in the newborn compared to adults in Hampshire, Shropshire, and Suffolk sheep. Similar observations have been made by Becker and Smith (1950) on Corriedale, Dorset and Hampshire sheep.

MATERIALS AND METHODS

This study involves 96 two-year-old ewes, and 60 lambs produced by them. Two different breeds were used: A wool producer (Rambouillet) and a meat producer (Hampshire). Ten of each breed were used in 1962, 20 in 1963 and 18 in 1964. Some of these ewes did not have lambs and some had twins; but in no case were data collected on more than one lamb from a given ewe.

All the ewes were allowed to run together in a flock and were given hay and water at the Montana Agricultural Experiment Station for 30 days prior to exposure to the rams. After the end of this period, rams were allowed to run with their respective breeds for 20 days (just over one estrus cycle). During this period, the ewes were kept on hay and water. At the end of the breeding period, half of the ewes from each breed were fed at the level recommended by the National Research Council (NRC) (1957) for maintenance, the others were fed two-thirds of that amount. Thus it is evident that all animals were fed at levels below that recommended for pregnant females. Each animal was placed in an individual pen and was fed a measured amount of feed; she was allowed access to this food for a period of about eight hours. During the remaining periods each day she had access to free running water but no feed.

The two levels of feeding were continued for 90 days, at which time half of the ewes from each breed who had been getting feed at a given level were shifted to the other level. Thus there were four feed regimens: (1) the NRC Standard throughout gestation (referred to as high-high); (2) NRC Standard for 90 days and two-thirds of the NRC Standard for the

rest of the gestation (referred to as high-low); (3) two-thirds of the NRC Standard for 90 days followed by the NRC Standard for the rest of the gestation (referred to as low-high); (4) two-thirds of the NRC Standard throughout gestation (referred to as low-low).

The ewes were weighed on the day the feed regimens were started, on the day changeover was made, and four days after parturition. The weight of each lamb was recorded 24 hours after its birth.

Blood samples were collected from each ewe at the beginning of the feed period (hereafter referred to as 0-Time), at the change (hereafter referred to as 100th-Day) and 24 hours after parturition (hereafter referred to as post-partum). Blood samples from lambs were taken at 24 hours of age. These blood samples were used to determine hemoglobin, hematocrit, hematocrit to hemoglobin ratio, total white cell count and differential white count. Another sample taken at four days of age was used to determine total plasma protein, albumin-globulin ratio and thyroid level, as were the three sets of samples taken from the ewes.

The total plasma protein was determined by Lowry's method (1951). Albumin-globulin separation was accomplished by disc-gel electrophoresis using the technique described by Davis (1964). Evaluation of the gel was done by Joyce-Chromoscan Densitometer in which approximately 30 gammas of protein proved to be the highest usable amount.

Thyroid function was indicated by serum protein uptake of I^{131} triiodothyronine from impregnated resin IRA 400 as described by Sterling and Tabachnick (1960).

Oxygen utilization was determined on one lamb from each ewe at the end of the first four 24 hour periods. The methods and results of these determinations have been submitted for publication elsewhere, but will be referred to in this report.

RESULTS

The mean values of 10 physiological parameters measured in the ewes and lambs of Rambouillet and Hampshire sheep are presented in Table I. Since the mean values given are from pooled data obtained in three different years and following two different feeding regimens, statistical evaluation required an analysis of variance and co-variance using the following heirarchial classification:

Between years
Between breeds within years
Between feed level within breed within years
Within feed level within breed within years

No effect of feed level was indicated, however, several statistically significant breed differences were evident (Table II).

In order to illustrate the indicated breed differences more clearly, and to approach the question of temporal variations in these breed differences, the data of Table I are presented again in Table III in the form of ratios between the mean value for Rambouillet ewes and that for Hampshire ewes for each parameter; and between the mean values of the ewes of a given breed and that of the lambs of the same breed. From Table III it can be seen that although at 0-Time the Hampshire breed was higher in total plasma protein, total WBC count and lymphocyte percentage, they gave birth to lambs with lower values.

In order to illustrate more clearly the pattern of changes during advancing gestation and the relation between the level in the dam and that in the newborn, the data of Table I were used to calculate another set of relative values. These values were obtained by dividing the absolute values at 100th-Day of gestation, post-partum and in the newborn into

the first collection of the dam. From Table IV, it can be seen that Rambouillets seem to decrease less in those characteristics which had a tendency to decrease and increase more in those that showed increase.

The extent to which the genetic background of the breed affects (a) the values of a given characteristic at two stages of gestation, (b) the value of a given characteristic in the offspring relative to that at various stages of gestation of the dam, (c) the value of one characteristic in the lamb relative to the value of a second characteristic in the lamb and (d) the value of one characteristic of the dam with a second characteristic of the dam at a given stage of gestation was estimated by calculating the between breed correlations, which were obtained as follows:

$$\frac{\sigma_{xy} \text{ attributable to breed difference}}{\sqrt{\sigma_x^2 \sigma_y^2} \text{ attributable to breed difference}}$$

where x and y are the characteristics being considered.

For example, hemoglobin 0-Time and hemoglobin 100th-Day or hemoglobin 0-Time and total plasma protein 0-Time. It is assumed that the environmental factors which influence these relationships in a positive direction and those which influence them in a negative direction will tend to neutralize each other, thus leaving a clearer picture of genetic influence.

The results of those between breed correlations involving one characteristic at various times are shown in Table V; those involving two characteristics at a given time are shown in Table VI. The corresponding within breed correlations, which were obtained as follows:

$$\frac{\sigma_{xy} \text{ within breeds}}{\sqrt{\sigma_x^2 \sigma_y^2} \text{ within breeds}}$$

where x and y are the characteristics being considered, are shown in Tables VII and VIII.

A comparison of Table V with Table VII as well as Table VI with Table VIII, shows that almost invariably the correlations within breeds are smaller than those between breeds. This difference in magnitude is not unexpected, as the within breed correlations are more affected by environmental factors. Most of the exceptions are in lambs, thus pointing to the complex physiological state of the neonate.

TABLE I

THE MEAN VALUES FOR VARIOUS CHARACTERISTICS IN TWO BREEDS OF SHEEP

			Total Plasma Protein	WBC/ cu.mm.	Poly-morphs %	Lympho-cytes %	Thyroid Level	Hemoglobin gm/100 ml.	Hemato-crit %	Hematocrit / Hemoglobin	Weight	A/G
Ewe	0-Time	H	463*	7575	30	61	36**	13.5	40.1	2.97	117.7 Lbs.	1.667
		R	417	6677	32	56	34	12.7	39.8	3.13	115.8 Lbs.	1.839
	100th-Day	H	415	6566	25	64	35	12.5	37.2	2.97	--	--
		R	380	6154	29	57	36	11.6	36.3	3.13	--	--
	Post-Partum	H	360	7675	34	57	44	11.4	34.9	3.07	110.7 Lbs.	1.357
		R	335	7682	42	48	46	11.0	35.0	3.18	102.9 Lbs.	1.510
Lamb		H	323	5486	50	45	39	14.1	46.8	3.32	4126.3 Gms.	1.667
		R	349	6661	51	45	41	13.7	43.6	3.17	4041.2 Gms.	1.404

* Amount of protein in gammas in 5 λ of plasma

** Counts of I^{131} in unit of 100

H Hampshire

R Rambouillet

TABLE II

F-VALUES ASSOCIATED WITH THE EFFECT OF BREED ON VARIOUS CHARACTERISTICS AT THREE STAGES IN THE ADULT AND IN THE NEWBORN

	EWE			LAMB
Characteristic	At 0-Time	At 100th-Day	After Partur-ition	
Total Plasma Protein	6.77**	2.30	1.69	0.35
Total WBC	6.28**	0.28	0.55	0.63
Polymorphs	1.19	2.38	0.49	1.17
Lymphocytes	3.06*	0.84	2.52	0.69
Thyroid Level	1.10	0.26	2.07	0.73
Hemoglobin	7.76**	9.00**	1.45	0.67
Hematocrit	0.90	2.70	0.50	1.68
A/G Ratio	0.26	---	0.33	2.66
Birth (Single or twin)	---	---	---	2.99

** Significant at the 1% Level

* Significant at the 5% Level

TABLE III

COMPARISON OF VARIOUS CHARACTERISTICS OF RAMBOUILLET AND HAMPSHIRE

Characteristic	EWE : EWE			LAMB: LAMB	LAMB : EWE	
	At 0-Time	At 100th-Day	Post-Partum		H	R
Total Plasma Protein	0.892*	0.895*	0.954*	1.0996*	0.686**	: 0.845**
Total WBC	0.959	0.935	1.006	1.068	0.861	: 0.959
Polymorphs	1.286	1.120	1.173	0.983	1.847	: 1.412
Lymphocytes	0.856	0.901	0.840	1.000	0.731	: 0.854
Thyroid Level	0.918	0.857	1.039	1.096	0.994	: 1.189
Hemoglobin	0.898	0.835	0.927	0.939	1.073	: 1.122
Hematocrit	0.941	0.883	0.979	0.919	1.205	: 1.177
A/G Ratio	1.103	-----	1.112	0.842	1.000	: 0.763

* In each case the Hampshire was used as the standard and given a value of 1

** In each case the dam was used as the standard and given a value of 1

H Hampshire breed

R Rambouillet breed

TABLE IV

COMPARISON OF TWO BREEDS OF SHEEP AS REGARDS THE PATTERN OF CHANGES IN VARIOUS CHARACTERISTICS DURING ADVANCING GESTATION IN THE DAM, AND IN THE NEWBORN

Characteristic	EWE				LAMB	
	100th-Day		Post-Partum			
	H	R	H	R	H	R
Total Plasma Protein	0.891*	0.893	0.766	0.819	0.686	0.845
Total WBC	0.937	0.914	1.130	1.185	0.861	0.959
Polymorphs	0.920	0.801	1.393	1.270	1.847	1.412
Lymphocytes	1.032	1.086	0.870	0.854	0.731	0.854
Thyroid Level	0.940	0.878	1.203	1.360	0.995	1.189
Hemoglobin	0.927	0.862	0.803	0.829	1.073	1.122
Hematocrit	0.922	0.865	0.829	0.862	1.205	1.177

* Values obtained by dividing absolute values at 100th-Day of gestation, Post-Partum, and newborn into first collection of dam.

H Hampshire

R Rambouillet

TABLE V

CORRELATION BETWEEN VALUES OF A PARTICULAR CHARACTERISTIC AT 0-TIME WITH 100TH-DAY, AT 100TH-DAY WITH POST-PARTUM, AT POST-PARTUM WITH LAMB, AND AT 0-TIME WITH LAMB BASED ON DIFFERENCE BETWEEN BREEDS

Characteristic	Between 0-Time X 100th-Day	Between 100th-Day X Post-Partum	Post-Partum X Lamb Characteristics	0-Time X Lamb Characteristics
Total Plasma Protein	.863**	.978**	-.830**	-.232
Total WBC	.719**	-.849**	-.363	-.816**
Polymorphs	.277	.425*	-.625**	-.738**
Lymphocytes	.266	.524**	-.364	-.608**
Thyroid Level	-.613**	.497**	-.830**	.200
Hemoglobin	.995**	.654**	.431*	.988**

** Significant at the 1% Level

* Significant at the 5% Level

TABLE VI

CORRELATION BETWEEN VARIOUS PAIRS OF CHARACTERISTICS AT A PARTICULAR TIME DURING GESTATION AND IN THE LAMB BASED ON DIFFERENCE BETWEEN BREEDS

Characteristic	EWE			LAMB
	At 0-Time	100th-Day	Post-Partum	
Thyroid X Hemoglobin	-.837**	-.963**	.885**	.171
Thyroid X Total Plasma Protein	-.753**	-.751**	-.399*	-.697**
Thyroid X Total WBC	-.934**	-.255	.976**	-.926**
Hemoglobin X Total Plasma Protein	.985**	.900**	.064	-.985**
Hemoglobin X Total WBC	.974**	.504**	.762**	-.819**
Bodyweight X Hemoglobin	--	--	--	-.100
Bodyweight X Thyroid	--	--	--	.787**
Bodyweight X Total Plasma Protein	--	--	--	-.106
Hemoglobin X Oxygen Used 1/	--	--	--	.602**
Bodyweight X Oxygen Used 1/	--	--	--	-.706**
Thyroid X Oxygen Used 1/	--	--	--	.087

** Significant at the 1% Level

* Significant at the 5% Level

1/ 24 Hours after Birth

TABLE VII

CORRELATION BETWEEN VALUES OF A PARTICULAR CHARACTERISTIC AT 0-TIME WITH 100TH-DAY, AT 100TH-DAY WITH POST-PARTUM AND AT POST-PARTUM WITH LAMB BASED ON DIFFERENCE BETWEEN ANIMALS OF A GIVEN BREED

Characteristic	0-Time With 100th-Day	100th-Day With Post-Partum	Post-Partum With Lamb
Total Plasma Protein	.112	.038	-.284
Total WBC	.556**	.138	.144
Polymorphs	.214	.450**	.122
Lymphocytes	.319*	.383*	.218
Thyroid Level	-.093	-.335*	-.388*
Hemoglobin	.256*	.273*	.392*

** Significant at the 1% Level

* Significant at the 5% Level

TABLE VIII

CORRELATION BETWEEN VARIOUS PAIRS OF CHARACTERISTICS AT PARTICULAR TIMES DURING GESTATION AND IN THE LAMB BASED ON DIFFERENCE BETWEEN ANIMALS OF A GIVEN BREED

	EWE			LAMB
Characteristic	At 0-Time	100th-Day	Post-Partum	
Thyroid X Hemoglobin	-.226	-.409**	.105	.026
Thyroid X Total Plasma Protein	-.071	-.013	-.249	-.136
Thyroid X WBC	-.282*	-.179	.082	-.121
Hemoglobin X Total Plasma Protein	-.113	.011	.058	-.190
Hemoglobin X WBC	.027	.226	-.073	-.215
Bodyweight X Hemoglobin	--	--	--	.342*
Bodyweight X Thyroid	--	--	--	-.347*
Bodyweight X Total Plasma Protein	--	--	--	-.282
Hemoglobin X Oxygen Used 1/	--	--	--	-.535**
Bodyweight X Oxygen Used 1/	--	--	--	-.815**
Thyroid X Oxygen Used 1/	--	--	--	.141

** Significant at the 1% Level

* Significant at the 5% Level

1/ 24 Hours after Birth

DISCUSSION

A. HEMOGLOBIN AND HEMATOCRIT LEVEL

The significant breed difference in hemoglobin concentration found in this study is consistent with the findings of Loggins et al. (1960), who showed that Florida Native sheep have a higher hemoglobin level than Hampshires and Rambouillets. Genetic control of this characteristic has also been shown in cattle, chickens and horses by various workers as described in the review of literature.

The magnitude of genetic influence is not yet clear as several non-genetic factors are known to affect these characteristics. For example, during pregnancy there was a decrease in hemoglobin percentage and hematocrit level in both breeds in this study. To the author's knowledge, this is the first report in which comparisons of hemoglobin and hematocrit levels have been made using the same animals over a period extending from conception to post-partum, thus providing an opportunity for a more detailed study of changes in these characteristics, within breeds as well as between breeds, at various stages.

Effect of Pregnancy

The report of Ullrey et al. (1965b) involved three breeds of sheep (Hampshire, Shropshire and Suffolk) at various stages of pregnancy, parturition and parturition plus 14 days in a study of these two characteristics. Their results show that there were slight fluctuations during pregnancy and that the values were lower toward the end and at post-partum. This is consistent with the results of the present study. But a number of factors limit the value of their study as a basis of comparison of pregnant

and non-pregnant animals. These factors are: (1) the earliest observations made on the same ewes when non-pregnant were at 12 months of age, (2) the earliest post conception measures were at two months, (3) the pregnant and lactating ewes were two to five years old. Since they could not detect any significant breed difference, they show only pooled mean values thus there is no way to determine whether there was a breed difference in the relative changes which might have occurred during gestation.

Other studies also show a decrease in hemoglobin and hematocrit level in various organisms during pregnancy especially near parturition. Morris (1944) pointed out that hemoglobin level in cows shows slight fluctuations during pregnancy with a sudden fall at 36 hours after parturition. Trum (1952) reported that there appears to be an anemia in late pregnancy in the horse. Bland et al. (1930) discussed the literature on this subject in humans in fair detail and mentioned that some workers have noted an increase, others have found no appreciable change and still others have noted a definite decrease in hemoglobin level in pregnant women. He concluded that in a great percentage of women, there is a decrease in hemoglobin level in pregnancy and to this the term "physiological anemia" has been applied.

Dieckmann and Wegner (1934) (cited by Trum, 1952) suggested that this change can be explained by an increase of 25% of blood volume in women at term. Strauss (1939) attributed this so-called "physiological anemia" of pregnancy in women to an approximate 20% increase in blood volume during the last trimester. He thinks that this "physiological

anemia" is only the effect of hydraemia.

In the author's view the etiology of lowered hemoglobin in late pregnancy is still not clear. Various workers have given opinions for and against the following possible causes.

1) The withdrawal of iron from the maternal corpuscles by the fetus (chlorotic origin)
2) The existence of hydraemia of pregnancy (plethora)
3) Progressive enlargement of vascular volume during gestation; a factor closely related to item number two.

Further investigation is required to throw light on the fundamental nature of the secondary or so-called "physiological anemia" of pregnancy. However, there are some indications of its nature from the results of the present study. Comparison of the decrease in hemoglobin concentration and hematocrit values during gestation disclose the following additional points of interest (Table I):

1) At 0-Time, Rambouillets required more hamatocrit to produce one unit of hemoglobin.
2) During the early part of gestation the decrease in hemoglobin concentration and hematocrit value was of the same magnitude in both breeds. Thus, the volume of hematocrit which produces one unit of hemoglobin at the 100th-Day was the same as at 0-Time in both breeds.
3) During advanced pregnancy, the Hampshire mother not only shows more decrease in hemoglobin compared to Rambouillet mothers, but

also more change in hemoglobin per unit of hematocrit relative to earlier stages. Kleiner and Orten (1962) claim that the cause of a hypochromic state due to iron deficiency is not uncommon during pregnancy. Guyton (1961) claims that, the level of iron in the body does not directly affect the total number of red blood cells produced, but the level of iron does greatly alter the quantity of hemoglobin that is available to fill the red blood cells. Consequently, when iron is deficient, the newly formed cells enter the blood stream in a hypochromic state. Bell et al. (1961) mention that in a mild iron deficiency the red cells may not be much reduced in number but each cell contains less than its normal complement of hemoglobin, that is, the mean corpuscular hemoglobin concentration is reduced.

4) The difference in hemoglobin concentration between Hampshire and Rambouillet ewes at 0-Time was approximately 6.3% but the difference in lambs of the two breeds was only 2.8%, thus indicating that Rambouillet mothers gave birth to lambs with a higher level of hemoglobin compared to themselves than Hampshire mothers did.

5) Rambouillet lambs have more hemoglobin per unit of hematocrit than Hampshire lambs. This relation was opposite in their dams at 0-Time.

Number 3, 4 and 5 above, strongly suggest that Rambouillet mothers metabolize their iron sources more efficiently and produce lambs with higher iron resources than Hampshire mothers do. In view of the importance of iron during pregnancy and the necessity of producing young with ample

stores of iron, in order that they can tide over the period during which the diet is exclusively milk, the Rambouillet mothers seem to be supplying a better physiological state. The existence of this difference in efficiency in utilization of iron by the Rambouillet breed was not only evident in the pooled data of the three years, but was consistent in each of the three years concerned.

Lambs of both breeds have a higher level of hemoglobin concentration and hematocrit value than their mothers. This observation is supported by the work of Ullrey et al. (1965b) in Hampshire, Shropshire and Suffolk sheep, Holz et al. (1961) and Reda and Hathout (1957) in sheep, and Anderson (1957) in the beagle dog.

B. LEUCOCYTE COUNTS

In the present study there was a statistically significant difference in total WBC count, Hampshire ewes being higher than Rambouillets (Table I). Similar genetic differences in total WBC count have been shown by Milicevic et al. (1960) and Tutikawa et al. (1958) among breeds of pigs and between strains of mice respectively. In the present study there did not appear to be any appreciable breed difference in neutrophil and lymphocyte percentages, which is consistent with the results of Todd et al. (1952), who found no genetic difference in neutrophil and lymphocyte percentages among breeds of pigs.

The post-partum values of total WBC count were higher in both breeds than at 0-Time or during pregnancy. Similar increases of WBC count in post-partum have been noted by Ullrey et al. (1965a) in Hampshire, Shropshire

and Suffolk breeds of sheep, and by Kerr et al. (1951) in cows; Luke (1953) showed that this picture can be duplicated by the injection of ACTH or adrenal cortex extract in non-pregnant pigs. Straub et al. (1959) suggested that the picture is one of mild or moderate stress. If it can be assumed that this effect is exclusively produced by, and directly proportional to the amount of adrenal cortex secretion, then it appears that Rambouillet mothers reacted to the stress of parturition by secreting more corticoids than the Hampshires did.

It is interesting to note that Rambouillet mothers had lower levels at 0-Time than Hampshires, but at post-partum the level in the Rambouillet was higher, thus further indicating a possible adaptive superiority of the Rambouillet.

Ullrey et al. (1965a) pointed out that lambs have lower total WBC count at 24 hours after their birth than their mothers at parturition in three breeds of sheep, Hampshire, Shropshire and Suffolk. The results of the present study support this finding; the figures of Ullrey et al. (1965a) and the author's being in close agreement. However, the results of Josland (1933) and Reda and Hathout (1957) indicate that lambs have higher WBC counts than adults. The reason for such a conflict may be that the term "newborn" in the literature does not always mean the young one which has just been born. Ullrey et al. (1965a) pointed out that lambs between the age of one and two months show higher counts of WBC than adults. Thus the results of Josland (1933) and Reda and Hathout (1957) may really not conflict with the present results.

The ewes of both breeds show a lower percentage of polymorphs than of lymphocytes. Similar results have been described by Josland (1933) in New Zealand sheep and cattle, and by Todd et al. (1952) in Southdown and Hampshire ewes. Figures given by Todd et al. (1952) on neutrophil and lymphocyte percentages in Hampshires agree quite well with the figures of the same breed in the present study.

The post-partum picture was one of well marked lymphopenia and neutrophilia. The same thing has been shown in swine, cattle and sheep by Luke (1953), Kerr et al. (1951), Ullrey et al. (1965a) respectively. The young ones were born with a higher percentage of polymorphs and a lower percentage of lymphocytes. This is consistent with the results of Ullrey et al. (1965a) in sheep and Gardiner et al. (1955) in pigs, who pointed out that among leucocytes, the most striking change was the shift from an excess of neutrophils at birth to an excess of lymphocytes with increasing age.

The lambs of the Rambouillet breed were higher in total WBC count and lymphocytes than the Hampshire lambs, in spite of the fact that their mothers showed the opposite relation at 0-Time and at the 100th-Day of pregnancy. This points to the fact that the Rambouillet sheep can not only show an increase in WBC count compared to the Hampshire, but can produce lambs with higher total WBC count, thus giving an apparent advantage, through this physiological characteristic, to their young at birth.

There was no detectable effect of feed on total WBC count, neutrophils or lymphocytes in either breed under study.

C. THYROID ACTIVITY

There was little difference in thyroid activity in the two breeds studied. This observation is consistent with the observations of various workers. For example, no difference in thyroid secretion rate has been found in certain breeds of cattle as reported by Lewis and Ralston (1953) and Sorensen (1958). Okamoto et al. (1961) and Kawecka (1962) showed that thyroid activity does not differ among breeds of chickens. The same has been shown by Matsuo (1961) among various strains of mice.

There did not appear to be any appreciable difference in thyroid secretion rate between the 100th-Day of pregnancy and 0-Time in either breed, a condition which has been noted by various workers as described in the review of literature.

At post-partum, thyroid activity was lower compared to 0-Time and the 100th-Day. The lowered activity of the thyroid gland could be due to a seasonal effect, however. Animals were bred in a colder season with shorter days and lambed in a season with warmer, longer days. Both temperature and day length have been shown to affect thyroid secretion. Hoersch et al. (1960) have demonstrated that by increasing the illumination from four to 12 hours, thyroid activity of sheep was progressively depressed. Decrease in thyroid secretion in a season with warmer, longer days, has been reported by Griffin et al. in Hampshire and Shropshire sheep, by Henneman et al. (1955) in Shropshire sheep, and in cattle, goats and

chickens by various workers as described in the review of literature.

That thyroid secretion rate decreases as the ambient temperature increases has also been shown by Hoersch et al. (1960) and Brooks et al. (1952) in sheep, and by Johnson (1958) and Thompson et al. (1963) in cattle.

Rambouillet lambs were born with a somewhat higher thyroid secretion rate than Hampshire; however, this difference was not statistically significant.

Statistical analysis indicated no effect of feed level on thyroid secretion. This observation is supported by the work of Hatch and Stroble (1963). These workers also could not find any difference in thyroid response in sheep between 66.67% and 100% of the NRC recommended level of feed.

From the above discussion, it must not be concluded that thyroid secretion is not under genetic control. Genetic control of thyroid secretion rate has been reported in sheep, cattle, pigs, chickens and mice by various workers.

D. BLOOD PLASMA PROTEINS

The statistically significant difference in total plasma protein between the adults of the breeds, Hampshire being higher in level, is in agreement with the genetic differences shown among breeds of cattle, and between ethnic groups of women.

By the 100th-Day of pregnancy there was a decrease in total plasma protein in both breeds. Ullrey et al. (1964) found a similar decrease at

about the same stage of pregnancy in Hampshire, Shropshire and Suffolk breeds of sheep. Peterson et al. (1961) found a decrease in plasma protein in pregnant hamsters. However, the fact that this occurrence is not true of all mammalian forms is indicated by the work of Leyssac (1960) and Stankiewiez et al. (1960) who pointed out that in pregnant women and in horses the concentration of total protein remains unchanged throughout gestation. The apparent inconsistency could be due primarily to differences in species in view of the failure of various workers (Blincoe and Brody, 1949 & 1951, Howes et al. 1957, Bedrak et al. 1956) to find any influence of temperature or of marked (50%) decrease in level of protein intake in cattle. However, other factors may be contributing.

Such a decrease in plasma protein during pregnancy could be due to the fact that there is competition between fetal and maternal tissue for available nutrients, the intensity of this competition being higher as the fetus increases in weight. It is evident that during the period in which the fetus is increasing in mass most rapidly, there is a higher demand for nutrients from the mother. Thus if the supply of diet to the mother is limited, the mother may have less available nutrients for her own sustenance. Further indication of this may be gleaned from the fact that Ullrey et al. (1964) found an actual increase in total plasma protein during the early days of pregnancy. This increase is presumably the result of the physiological adaptation of the dam to the sudden change in physiological state associated with the implantation of the zygote.

If such a pattern of change proves to be consistent, the level of plasma protein could possibly serve as an index of fetal growth. However, since the decrease is not likely to be linear, more work both on fetal growth and plasma protein concentration would be necessary before any such index could be applied. Nevertheless, the fact that the data from this study as well as those from the work of Ullrey et al. (1964) show that the lowest level of plasma protein exists at the termination of pregnancy adds support to this proposition.

There are four additional points of interest in Table I:

1) The reaction of the two breeds to pregnancy, as regards plasma protein concentration was differential, i. e. Rambouillets did not show as great a decrease as the Hampshires under similar conditions of handling and feeding.
2) Lambs of both breeds were born with lower plasma protein levels than their mothers had at 0-Time.
3) Lambs of the Rambouillets were born with higher total plasma protein than their mothers at post-partum. However, this was not so with the Hampshire breed.
4) In spite of the fact that Hampshire ewes were higher to start with and were higher throughout pregnancy, they gave birth to lambs with lower plasma protein than Rambouillet ewes did.

The existence of lower levels of total plasma protein in the newborn as compared to their mothers, has been shown by Ullrey et al. (1964) in Hampshire, Shropshire and Suffolk sheep, Smith (1950) in sheep, Dutta-

Chaurhri et al. (1959) and Stainer et al. (1954) (as cited by Carr and Gelfand, 1960) in the human, and Becker and Smith (1950) in Corriedale, Dorset and Hampshire sheep. This is consistent with the present findings on the Hampshire breed, but is in conflict with the present findings on Rambouillets. While studying the total concentration of serum protein and plasma volume in the rabbit neonate, Deichmiller and Dixon (1960) observed that neonates have a plasma volume up to one and one-half times greater per unit of body weight than the adults. They suggested that the low concentration of plasma protein in neonates can be explained by the difference in plasma volume between adult and neonate. However, such an explanation cannot be considered applicable to all organisms as evidenced by the present findings regarding Rambouillet sheep, and the findings of Karik and Hipsley (1961) who failed to find any difference in mean level of total serum protein in New Guinean mothers and their infants or Australian mothers and their infants.

In both breeds, there was a decrease in A/G ratio at post-partum compared to 0-Time. Some evidence of a relative change in the protein fraction has been described by Peterson et al. (1961) in hamsters. They pointed out that there is a decrease in albumin during pregnancy with the mean decreasing from 69.94 to 45.56. Among the globulin fractions the α- fraction increased markedly but no appreciable change in the β- fraction was found. The changes in the other globulin fractions were variable.

In the present study, Hampshire lambs were born with the same A/G ratio as their mothers had at 0-Time, but higher than their mothers had at post-partum. It is interesting to note that Rambouillet lambs have deviated from this pattern and were born with lower A/G ratio than their mothers had at either time. The fact that the globulin fractions are important in the immunity mechanisms strongly suggests that Rambouillet mothers provide better natal conditions than Hampshire mothers do. In view of the fact that Rambouillet and Hampshire mothers used in this study were raised under the same management, as part of the same flock, the probability that the differences in change from newborn to adult are environmental is small. Further question is raised as to the validity of the conclusions of Carr and Gelfand (1960). These two workers found close agreement between the figures obtained for European and African human cord blood sera and suggested that differences that occur later in life are not due to genetic factors. It appears that they assumed that in an organism at birth, all genes are functioning and remain so for the rest of its life and any change in phenotypes at a later date is only an environmental modification. It is known that some genes start their function at later stages of life and others are shut off. They attributed the difference in serum protein of European and African mothers to diet or parasitic infection, but in the present study there is no difference in serum protein between 100% and two-thirds of the NRC recommended feed allowance, nor could Howes et al. (1957) find any difference in total serum protein between a diet providing 50% of the NRC recommended protein

allowance and one providing 100% in Hereford and Brahman cattle. These studies raise further questions concerning the interpretation of Carr and Gelfand.

E. GENERAL DISCUSSION

Living organisms display a variety of methods of adapting to changes in their environment. Some of these methods are known to be genetic in origin, and to the extent that genetic variability exists in a population, will differ from one individual to another, and from one subgroup to another. Such differences in genetically based adaptations may not be evident when the various subgroups are kept under relatively constant environmental conditions. It is possible to have genetic differences evident under one set of conditions and not evident under another. This phenomenon was evident in several characteristics studied in this investigation. For example, in the stage immediately following conception there was a breed difference in level of hemoglobin, hematocrit, total WBC count, lymphocytes and total plasma protein as well as in the albumin to globulin ratio. As has been pointed out in the individual discussion sections, several of these differences disappeared as pregnancy advanced. No one of these changes was statistically significant ($P \geq .05$) although most of them approached it ($.10 > P \geq .05$). However, the probability that chance could account for the repeated occurrence found here is extremely small.

Of course, the fact that certain genotypes are more suited to a particular environment than others forms the basis of all evolutionary change. Furthermore, this phenomenon is utilized by breeders. For example,

it is well known that European evolved cattle are not adapted to tropical conditions; and the plant breeders frequently recommend certain varieties for one specific area, but not for others.

There is an evident difference between the breeds in the present study, in their reaction to pregnancy. In general Rambouillet ewes did not decrease as much in various traits under study which had a tendency to decrease and increased more in those which showed increase. This is especially evident in advanced gestation. It is possible that under mild stress, genes of one breed may prove better or as good as the other, but slight changes in the environment may bring additional genes into operation in one breed but not in the other, thus the former may prove more adaptive. It is not suggested that a dormant gene suddenly starts to act and creates a change all by itself. The whole complex of existing physiological entities may be involved. Thus the effect of one gene will be superimposed upon that of a second, and they in turn, on a third. The exact nature of such changes, of course is not known. The best that can be done at present is to take quantitative measurements of various physiological characteristics and try to make reasonable conclusions about the over-all complex involved. Physiological changes, or differences in such physiological changes in two genotypes may be used as a basis of speculation concerning evolution.

Rambouillet ewes showed more tolerance to pregnancy and thus may be considered more adaptive. If the abilities to make such physiological adjustment have a heritable basis, it is reasonable to conclude that the

underlying genetic constitution concerned with the ability to adjust must have arisen through evolution. The breeds used here are believed to have different evolutionary histories. Differences in various physiological parameters and adaptations would normally be expected between such groups; however, it is not possible to discuss the results of the present study in relation to the historical backgrounds of these breeds due to two main reasons. (1) The knowledge of the histories of the breeds is not adequate. (2) The discussion will have to be based upon suppositions, as little is known about the effect of various environmental factors on physiological parameters.

The greater adjustment made by the individuals of the Rambouillet breed in response to pregnancy is only one facet of the present report, another aspect is the fact that Rambouillets gave birth to lambs with higher total plasma protein, total WBC count, lower A/G ratio and hyperchromic hemoglobin. If the smaller drop in plasma protein during later stages of pregnancy, shown by Rambouillet ewes is related to the fact that Rambouillet lambs were higher in total plasma protein and hemoglobin; one may be justified in concluding that more amino acids are available (plasma proteins are fairly labile) to Rambouillet fetuses. This ability to utilize protein, which is exhibited by the Rambouillet breed was dormant until the stress of pregnancy came into play.

The higher value of various characteristics in Rambouillet lambs may be the result of differences in placenta permeability or any of several other factors. Little more can be said on this matter as the physiological

functions of the neonate are not well understood.

Another example of different reactions of two genotypes to the same environment and different reactions by the same genotype to different environments is evident in the study of Blackmore and Phalora (manuscript in preparation). This study of oxygen consumption was done on the same lambs which were used in the present study to measure hemoglobin, total WBC count, total plasma protein, etc. The rate of oxygen consumption of some lambs was measured in a small dark chamber and the rest in a large well-lighted chamber. The results indicate that every lamb of the Rambouillet breed had reached its peak use by the second day, but lambs of the Hampshire breed reached their peak on the third day when measurement was made in the dark small chamber. When measurement was made in the large chamber however, most of the Rambouillets had reached their peak on the first day and some of the Hampshires did not reach their peak until the fourth day. There was only one lamb that was not characteristic of its breed; that was a Hampshire which was losing weight. It reached its peak on the second day. Otherwise, there was complete breed separation. A total of 39 Hampshires and 37 Rambouillets were involved.

By eliminating the breed difference from the data by statistical analysis, additional interesting points were disclosed. Table VIII presents correlations between pairs of characteristics at a given stage of pregnancy and in the newborn within breeds. The results show that almost invariably the correlations within breeds is smaller than the corresponding ones between breeds (Table VI). Almost invariably the sign of the

correlation is the same within breeds as between breeds. Whenever there was a shift of sign in a given pair of characteristics, the shift was the same both within and between breeds. The predictability of this phenomenon indicates that the characteristics are under genetic control.

It is reasonable to suppose that the gene frequency for certain characteristics is different in different breeds and this difference is larger between groups than within groups. Thus the degree of association of the characteristics will be greater between groups than within groups. When the difference which exists in two groups was removed by statistical analysis, the value of the correlations dropped. This is not unexpected and is evidence that the characteristics are controlled genetically.

The above discussion also holds true for Tables V and VII, in which one characteristic is compared at different stages of pregnancy within breed.

In both the tables, the exceptions are mainly in lambs, which is suggestive of the complex nature of functions in the neonate. This goes along well with the conclusions drawn from the observations on oxygen utilization of lambs.

The evidence is consistent with the idea that Rambouillet lambs are better adapted on their first day of life than Hampshire lambs. The higher values of globulin, total WBC count and lymphocytes of Rambouillet lambs could be taken as an indication that they were better equipped with defensive mechanisms at the time of birth. The fact that in two years under identical care and handling of both breeds, two sets of twins and eight

single lambs from the Hampshire breed died by the end of the first day, while during the same period only three lambs died from the Rambouillet breed (all of the latter were members of sets of twins, the other member surviving in each case) lends additional support to the proposition. On the other hand, Hampshire ewes lost less weight during pregnancy than Rambouillets; but the average weight of lambs compared to mothers, breed by breed, is almost the same. This observation of less weight loss by Hampshires during pregnancy is indicative of more efficient use of energy by the breed - a quality certainly important for a meat producing breed.

Intrauterine environments are complicated and as yet very little explored. The author is not aware of any report in the literature in which the maternal influence on the neonate has been studied on characteristics other than size and growth. Reports by Hunter (1956) on sheep, and by Brumby (1960) and McLaren and Michie (1960) on mice are representative of the studies of maternal influence on neonate size. Brumby (1960) elegantly demonstrated an intrauterine effect on growth by implantation of both large and small strain eggs into unselected strain females and comparison of the growth of the resultant embryos with the control stocks of the large and small strains. The large and the small strain animals were found to increase greatly in size when implanted into females of the unselected strain, even though the unselected strain females were smaller in size than the large strain females. It follows that the maternal environment provided by the large strain female must be inferior to that provided by the unselected females.

It seems reasonable to suppose that if a complex characteristic like growth, which is the result of physiological activity of many tissues and has a multiple factor inheritance, could be influenced by intrauterine environment, certainly other physiological characteristics like total plasma protein, hemoglobin level, etc., might be subject to such influence as well. Some of the possible ways in which prenatal maternal influence is exerted are relevant to the present study.

I. The competition between fetus and maternal tissue. Available nutrients could be a factor in the mechanism of maternal influence. It seems reasonable to conclude that this influence is greater in species having a longer gestation period, as the fetus competes with the maternal tissue longer. In this connection, the present study provides an interesting observation, as Rambouillet ewes which give birth to lambs which seem better adapted to the sudden change in environment have a longer gestation period. Although all the difference cannot be explained by the longer gestation period in Rambouillets, it may be one of the contributing factors.

II. Maternal Hormonal Control. The fetus is dependent on the mother for various hormones, especially in the early stages of development, for example, hemopoietic factor and other factors concerned with the formation of blood. Any breed difference in blood forming efficiency which is dependent on these factors could be reflected in the fetus. Another example can be cited from the work of Cote (1954) (cited by Hunter, 1956). He pointed out that injection of a preparation of purified growth hormone during pregnancy increased the weight of the young at birth. Although

there is no reason to suppose that the level of growth hormone in the lambs is directly affected by some hormonal level in the dam, the possible influence of some physiological agent in the dam on the function of the lamb cannot be excluded, especially in view of evidence in the literature indicating that the physiological well-being of a dam may have a direct effect on the growth of the offspring (Blackmore et al. 1958).

III. Placenta. The most important element in the environment of a fetus is the placenta. It is of dual origin, part fetal and part maternal. The placenta is the digestive system, respiratory system, excretory system and endocrine gland for its fetus. It is responsible for the entire transfer of nutrients from the mother to the fetus. Any breed difference in the permeability of placenta can produce a difference in the amount of nutrients available to the fetus.

IV. Blood Supply. The amount of blood passing through the placenta could be influenced by the caliber of the umbilical vessels, blood pressure in them, and the amount of amniotic fluid. Differences in any of these could make a significant difference in the amount of nutrients and various other factors reaching the fetus.

SUMMARY

Two breeds of sheep, whose origins have been tentatively traced to different areas of the world, were used. Two-year-old ewes and lambs produced by them represented the two breeds as follows:

1962	10	Rambouillets and	10	Hampshires
1963	20	"	20	"
1964	18	"	18	"

The ewes were kept together in one flock for 30 days prior to the introduction of rams. The breeds were separated and the rams run with their respective breeds for the next 20 days. During the next 90 days half of the ewes from each breed received feed at the level recommended by the National Research Council. The rest received two-thirds of that amount. Half of the ewes of each breed on a given feed level were then shifted to the other feed level for the remainder of the gestation period. Thus four feed regimens were used for each breed. All ewes on a given feed regimen were run together regardless of breed.

The following measurements were made on the ewes at the start of the feeding program, at the time of change-over, and one day after parturition: hemoglobin, hematocrit, hematocrit to hemoglobin ratio, total plasma protein, albumin to globulin ratio, total WBC count, polymorphs, lymphocytes, thyroid level and weight.

The following measurements were taken on the lambs (one lamb per ewe): hemoglobin, hematocrit, hematocrit to hemoglobin ratio, total WBC count, polymorphs, lymphocytes, weight and oxygen consumption at one day of age; total plasma protein, albumin to globulin ratio and thyroid level, at four days of age.

The Hampshire ewes showed higher levels (statistically significant) in total plasma protein, total WBC count, lymphocytes and hemoglobin, at the beginning. They were also higher (but not statistically significant) in hematocrit and body weight. They were lower (but not statistically significant) in albumin to globulin ratio, hematocrit to hemoglobin ratio and in polymorphs.

During parturition the Hampshires sustained a greater decrease in total plasma protein, hemoglobin and hematocrit; a lesser decrease in lymphocytes, albumin to globulin ratio and weight; a greater increase in hematocrit to hemoglobin ratio; and a lesser increase in polymorphs and total WBC count.

The differences between the two breeds had actually been reversed in total WBC count and hematocrit; but there were no statistically significant differences at parturition.

The Hampshires gave birth to lambs with higher hematocrit, hemoglobin, hematocrit to hemoglobin ratio, albumin to globulin ratio and weight, but lower in total plasma protein, total WBC count and polymorphs.

The Hampshires showed higher lamb to ewe ratios in polymorphs, hematocrit, hematocrit to hemoglobin ratio and albumin to globulin ratio; but lower lamb to ewe ratios in total plasma protein, total WBC count, lymphocytes and hemoglobin.

The lambs were actually higher than the ewes in polymorphs, hemoglobin and hematocrit for both breeds.

In two years under identical care and handling the Hampshires lost two sets of twins and eight singles by the end of the first day. During the

same period the Rambouillets lost only three lambs. All three of the latter breed were members of sets of twins, the other twin surviving in each case.

The following general conclusions seem justified:

1) Gene frequency in total plasma protein, total WBC count, hemoglobin, hematocrit and albumin to globulin ratio is distinctly different in the two breeds.

2) The Rambouillet breed could withstand the stress of pregnancy better than the Hampshire.

3) The Hampshire ewes use their energy more efficiently as far as their own maintenance is concerned.

4) The Rambouillet lambs showed better adaptation on their first day of life. Thus it appears that the Rambouillets may be providing better intrauterine environments and/or Rambouillet fetuses have better biochemical status as indicated by their higher value of total plasma protein, total WBC count, lymphocytes and hemoglobin, and lower value of albumin to globulin ratio.

5) Genetic differences could be evident under one environment and not evident under another.

6) Although it is known that genetic differences exist because of differences in environmental history, it is impossible to discuss these differences between these two breeds in relation to their environmental history because so little is known about the origin of these two breeds.

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