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PHENOTYPIC AND GENETIC ASSOCIATION BETWEEN PRODUCTION/ REPRODUCTION TRAITS AND BLOOD BIOCHEMICAL POLYMORPHIC CHARACTERS IN FINNSHEEP

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Preface

Many people have helped me in various ways, to all of whom I should like to express my thanks. My supervisor, Professor KALLE MAIJALA, Head of the Department of Animal Breeding, University of Helsinki, has from the start followed the progress of the study. His continuous and stimulating criticism have been of great value, and I am very thankful for this.

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Vantaa April, 1979 FAIK ATROSHI

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1. INTRODUCTION

Mendel identified the factors we know as genes and Darwin realized the biological importance of natural selection in biological evolution, but it was EHRLICH and MORGENROTH in 1900, who revealed the differences between the blood groups of farm animals in goats.

Polymorphism, a phenomenon which is widespread in nature, was defined by FORD (1945) as the existence in a given population of multiple genetic variants in frequencies greater than can be accounted for by recurrent mutation pressure. Since the discovery of inherited biochemical polymorphism in cattle, sheep and poultry, interest has centred on the possibility of a relationship between various polymorphic characters and production characters, or the ability of the animal to do well in a particular environment. Relationships such as these are of interest both from the point of view of providing a physiological basis for productive differences and, hopefully, as a basis for more accurate and/or earlier selection of animals for various production traits.

Within a species, any observed differences in metabolism might be due to genetic effects or environmental influences, or both. The first step in any attempt to breed for improvement is to identify and separate these factors as far as possible. Differences solely due to environment can be recognized because they are altered by environmental changes. Genetic differences on the other hand are to a variable degree inherited from one generation to the next. If inheritance accounts for the majority of any observed variation, offspring will resemble their parents; if the variation is due to environmental factors then offspring would no more resemble their parents than do unrelated animals. Estimates of heritage are usually based on such comparisons and often both inheritance and environment interact to produce the observed character. Generally speaking the broader the trait under investigation the more difficult it will be to separate these effects and the more complex the genetic control is likely to be. MORTON et al. (1964) indicates that complex interactions of natural selection and biochemical characters are responsible for the maintenance of polymorphism and the infertility and neonatal mortality as well as adult mortality, are the most likely characters with which associations will be found. In man, genetic differences in metabolism can be exemplified by any number of inborn errors of metabolism (BROCK and MAYO, 1972).

Several biochemical polymorphisms occur in the red cells and plasma of sheep. Four of these, haemoglobin, transferrin, glutathione and potassium have been the subject of considerable study, and their inheritance, chemistry and physiology have been reported in detail by several workers in this field.

The haemoglobin types are attracting particular attention at present because of evidence of a relationship between haemoglobin types and prolificacy and resistance to worm infection. There is accumulating evidence from Australia, the Federal Republic of Germany and the

United Kingdom (WALKER, 1976) that the haemoglobin type B gene favours the production of twins and the occurrence of higher flock culling and mortality rates. Reliable reports from Australia and the United States of America show that susceptibility to haemonchosis is greater in sheep with type B haemoglobin than those of type A. There is also the suggestion (EVANS and TURNER, 1965) that when a breed is taken from its native environment and established in a different environment the gene frequency of B alters, suggesting that the relative advantage and disadvantage of haemoglobin A and haemoglobin B also alter.

Transferrin is the iron-binding protein of the blood plasma and in many species of mammals it exists in two or more genetically controlled variant forms. There is considerable variation among sheep breeds in the frequency of the transferrin alleles, each responsible for the formation of one type of transferrin. It is quite possible that this variation is not only due to the breed but can also be attributed to factors relating to the environment where sheep live, mainly latitude, altitude, climate, nutrition and parasites. Referring to the possible association of transferrin types and several quantitative traits, most of the workers suggest that the transferrin varieties of sheep appear to be associated with reproductive performance and, as already mentioned, may also have some adaptive significance.

Since the discovery of »glutathione instability» of human red cells in drug-induced haemolytic anaemia (BEUTLER, 1957) interest in the red blood cell has been growing in the function of reduced glutathione (GSH). It has been shown that GSH is involved in protecting haemoglobin against irreversible oxidation denaturation, guarding membrane lipids against peroxidation and shielding essential enzymes against inactivation (JAFFE, 1970).

The red cell GSH deficiency which is particularly prevalent in the Finnish sheep provides an example of a single gene effect which is probably detrimental to the individual. Such red cells have a life span which is at least 40 days shorter than normal (TUCKER, 1974) and there is evidence that sheep with this deficiency may be prone to anaemia. Since the chief function of GSH is to protect the cell against oxidative damage, it might be expected that GSH deficient cells (low-GSH) would not be able to withstand oxidative stress as well as normal red cells (high-GSH) (TUCKER, 1977).

Relationships between erythrocyte GSH levels and some production traits in animals (e. g. growth rate, body weight, fleece weight, milk yield, mortality) have been studied by various workers in this field.

The red cell potassium (K^+) polymorphism found in sheep, provides an example of how small genetic effects can be superimposed on major genetic differences so that the final phenotypic value measured represents the total effect of several gene influences. If blood K^+ concentration is measured in practically any breed of sheep, a discontinuous bimodel distribution is found. Some sheep have red cells with high K (HK-type) and some have cells with low K (LK-type). This difference is controlled by an allelic pair of genes, the gene for K^L being dominant over that for K^H. However, within these two major classes, minor differences can be detected which are also probably under genetic control. Within the HK and LK classes there are marked breed differences, and plasma K^+ concentrations may also be influenced by breed (TANEJA et al., 1969; EAGLETON et al., 1970). Many studies have been undertaken with sheep, correlating blood GSH and K^+ measurements, and factors which are of economic importance in the fields of husbandry and breeding have proved to be of a great practical value in view of the possibility of fixing the physiological traits through controlled breeding programmes.

The ability to identify such genes segregating in a population may be of help to the geneticist and breeder in three respects: (1) it is possible that the genotypes may differ in adaptive values which may be reflected in some economic characteristics of the animals; (2) these identifiable genes can be used as markers in genetic

studies and (3) since several alleles are generally present in a population, they can provide a valuable parentage check.

The purpose of the present study is: (a) to determine the population structure and geographical distribution in Finland of the haemoglobin, transferrin, potassium and glutathione loci in the Finnsheep, and (b) to investigate the relationship between the polymorphic alleles on the one hand, and productive and/or reproductive traits on the other.

2. REVIEW OF LITERATURE

During the last two decades facts illustrating the biochemical basis of genetic individuality have provoked much discussion as regards origin, maintenance and significance — discussion in which the precision of many of the basic observations has not always been sustained. This is perhaps inevitable, since there is such a fusion of disciplines occurring. However, current knowledge of physiology as pathology would be adequate to solve many of these problems.

Meanwhile, serological and biochemical marker gene techniques have been established as important tools of the animal geneticist. This thesis reviews what is currently known and available and points out some of the practical implications of these findings.

2.1. Haemoglobins

2.1.1. Haemoglobin types in sheep and their distribution

Haemoglobins (Hb) are protein molecules, each consisting of four polypeptide chains and one haem group per chain. These four chains usually occur in two identical pairs, namely the alpha (α) and the beta (β) chains, each having a different amino-acid sequence and each being under the control of separate non-allelic genes (TUCKER, 1971).

Two different haemoglobin types are found in the normal adult sheep (HARRIS and WARREN, 1955). EVANS et al. (1956) named them Hb A and Hb B. They correspond to the haemoglobins I and II described by van der HELM et al. (1957). Breeding data indicate that these types are genetically determined by two co-dominant autosomal alleles which produce three observable phenotypes, namely AA, AB and BB (EVANS et al., 1956; HUISMAN et al., 1958 b). Although the nomenclature (A, AB, B) has not always been the same, subsequent work has confirmed this original observation (HUISMAN et al., 1958 a; van VLIET, 1962; MEYER, 1963 b; DASSAT and BERNOCO, 1966; MEYER at al., 1967; AGAR, 1969). These haemoglobin types are distinguished on the basis of their electrophoretic mobility in starch gel, Hb A moving faster than Hb B (EVANS et al., 1956).

Additional haemoglobins are rarely found in sheep, namely Hb C or Hb N and Hb D. Hb C was reported in animals which were anaemic (BLUNT and EVANS, 1963; van VLIET and HUISMAN, 1964; BRAEND et al., 1964; BRAEND and EFREMOV, 1965; ARORA et al., 1970) or made anaemic experimentally (BEALE et al., 1966; MOOR et al., 1966; TUCKER, 1966; KITCHEN et al., 1968; AGAR and EVANS, 1969; BLUNT et al., 1969; NEETHLING et al., 1969;, AGAR et al., 1970) and also in certain non anaemic adult sheep (WILSON et al., 1966; ATROSHI et al., 1979). The electrophoretic mobility of Hb C is slower than that of Hb B (van VLIET and HUISMAN, 1964) and was found in animals of genotype AA or AB. Hb C occurred commonly in Norwegian sheep breeds (van VLIET and HUISMAN, 1964). Haemoglobin D was reported by VASKOV and EFREMOV (1967), to be in the apparently healthy Hb AB sheep. Hb D has

the fastest migration rate — faster than Hb A. This haemoglobin was, however, not detected in the offspring of the animals carrying it.

The distribution of Hb types in various sheep breeds living in different agroclimatic zones has been reported by different workers. According to EVANS et al. (1958 a and b), sheep in northern Europe tend to be Hb A type, whereas those in southern Britain, northern Africa and the Middle East were Hb B type. In a study of Southdown and Romney Marsh sheep in Australia, EVANS and BLUNT (1961), concluded that Hb A and AB sheep were better adapted to the environment of drought, parasitism and heat than were Hb B sheep. There are, however, four reports in the literature which do not support this view. DASSAT and SARTORE (1968), found no difference in the distribution of Hb type sheep in Sardinia which inhabit mountains, hills and lowland areas. DASSAT, (1964), reported that Hb B was common among sheep living in the hilly regions of Cuneo province of Italy whilst CHAN, (1968), working with Corriedale, Jonin and Criollo breeds in the Peruvian Andes has reported a preponderance of sheep with Hb B at these altitudes. AGAR, (1968), and AGAR and SETH, (1971), reported that Hb B confers an adaptive advantage in the relatively drier parts of India and this also holds true for the sheep breeds in the Himalayan region. It has been shown (PODGORNAYA, 1976) that sheep breeds in the Pamir highland (altitudes of 3 000—4 000 m) are mostly heterozygous. Generally, it seems that this polymorphic character has some adaptive significance (EVANS et al., 1958). For example, AGAR et al., (1972), suggest that flocks in which Hb A is predominant are confined to latitudes higher than 40°, whereas those in which Hb B is predominant appear to be distributed world-wide.

2.1.2. Physiological differences in sheep of different haemoglobin types

Since the discovery of haemoglobin polymorphism in sheep, attempts have been made to relate these polymorphic characters to other physiological characters. Perhaps the most important difference is in their oxygen affinities, Hb A having a higher affinity than Hb B, with Hb AB intermediate (HUISMAN et al., 1958 a; MESCHIA et al., 1961 a; DAWSON and EVANS, 1962; MESCHIA et al., 1961 b; NAUGHTON et al., 1963; BREATHNACK, 1964; SIRS, 1966; HOREJSI, 1970). The importance of this difference is that Hb B animals are more efficient in transporting oxygen than are Hb A animals because Hb B is able to liberate more oxygen per unit of Hb to the body tissues for a given drop in oxygen supply (DAWSON and EVANS, 1965). However, Hb A animals are able to compensate for this relative tissue hypoxia by adjusting their respiratory and circulatory systems (DAWSON and EVANS, 1965, 1967). DAWSON and EVANS (1966) examined the relationship between the oxygen affinity of a sheep's Hb and its cardiorespiratory responses to acute arterial hypoxia induced by a 20 min exposure to 9,3 per cent oxygen in nitrogen. It was found that Hb A sheep were more resistant than were the Hb B sheep. The authors concluded that the conditions under which the possession of the A gene would be expected to be advantageous to the sheep are those in which the oxygen uptake becomes more difficult, e.g. in mountainous regions.

The red blood cells of sheep of different haemoglobin types differ in several features. MOUNIB and EVANS, (1959), reported that in general, red cell density is related to Hb type (Hb A < Hb AB < Hb B). Haemoglobin A sheep have been found to have a larger blood volume (DAWSON and EVANS, 1965) and higher packed cell volumes (DAWSON and EVANS, 1965; MOUNIB and EVANS, 1959) than the Hb B sheep. KHATTAB et al., (1964), claimed that the osmotic fragility of red cells with Hb A was greater than that of red cells with Hb B. The blood characteristics have been reviewed in greater detail by TUCKER, (1971). Haemoglobin B is less stable than Hb A and is easily denaturated and dissociated into sub-units (DAWSON and EVANS, 1962; SHREFFLER and

VINOGARD, 1962). MANWELL and BAKER, (1970), have speculated that sheep with Hb A have an advantage over Hb B sheep because less of their amino acid intake and energy production has to be used for the maintenance of the circulatory Hb levels. Support for this idea was given by the finding that Hb A sheep had greater fleece weights than Hb B sheep (WATSON and KHATTAB, 1964). Recent evidence (WIENER et al., 1974) indicates that a relationship may exist between Hb types and the copper levels in whole blood and most of the blood components. In a study of the Scottish Blackface, Cheviot and Welsh Mountain breeds the authors found that within breeds the Hb B type sheep had considerably higher levels of copper than Hb A sheep. Haemoglobin AB sheep were intermediate in this respect. The biggest differences were found in plasma levels (37 μg/100 ml and 19 μg/100 ml for Hb B and Hb A, respectively). This evidence is consistent with the existence of a gene with a marked effect on copper levels that is linked to the locus for Hb type.

The various types of haemoglobin sheep also differ in the concentration of potassium in their red cells. Usually, sheep show a bimodal distribution of the concentration of potassium in their red cells (EVANS, 1954), the two types being designated HK and LK. Although the genes responsible for potassium and Hb types are at independent loci (EVANS et al., 1956) sheep with Hb A in both HK and LK phenotypes have a higher mean red cell potassium value than those with Hb B, whereas the Hb AB individuals are intermediate (EVANS, 1961; KHATTAB et al., 1964 b). When frequencies of Hb and potassium types are compared, there is a strong correlation between them within British breeds (EVANS et al., 1958 a), in other words, a breed with a high Hb A frequency has a high HK type frequency whereas a low Hb A frequency is associated with a low HK type frequency. These findings have been confirmed in Italian Langhe sheep (DASSAT, 1964). EVANS et al., (1963), obtained evidence from worm egg counts at the height of anaemia and during postmortem that Hb A sheep are less susceptible to infection with *Haemonchus contortus* than Hb AB sheep. The authors related this difference to the oxygen dissociation curve, suggesting that at equivalent partial pressure, more oxygen would be liberated from Hb B than from Hb A. Hence, *Haemonchus contortus* in Hb B sheep would obtain more oxygen for respiratory purposes. NEETHLING et al. in South Africa, as reported by AGAR et al., (1972), JILEK and BRADLEY, (1969), in North America, and ALTAIF and DARGIE (1978 a, 1978 b and 1978 c), in Scotland, have confirmed this finding. AGAR et al., (1972), also reported that NEETHLING et al. obtained a correlation between a high incidence of the A gene and resistance to anaemia induced by selenium (Se) poisoning. Haemoglobin type has also been shown to have a marked influence on erythrocyte reduced glutathione (GSH) levels (AGAR et al., 1972) and the authors reported that in the GSH^H group Hb B animals tended to have a lower erythrocyte GSH value than did Hb AB animals, although contradictory results have been obtained by KALLA and GHOSH, (1973). The significance of such relationships remains obscure. On the relationship of haemoglobin types with haematocrit values MOUNIB and EVANS, (1959), show that Hb A sheep have higher haematocrit values than Hb B sheep.

2.1.3. The relationship between haemoglobin type and productive/reproductive performance in sheep

Generally, reported associations of Hb types with production characters have been varied and poorly defined. KING et el., (1958), in a study of Hb and blood potassium type of Scottish Blackface sheep, did not obtain a significant association with any character, including body weight and fleece weight of the ewe, plus the birth weight, body weight (at various ages) cannon bone length, modulation and mean fibre length of the progeny.

Similarly, MAYO et al., (1970), found no relationship between the Hb type and an array of production characters of Merino sheep. AGAR

and SETH, (1971), did not find any association between Hb type and wool production in Polwarth and cross-breeds of Polwarth and Rampur Busheir sheep. On the other hand, KALLA et al., (1971), KALLA and GHOSH, (1975), found that Hb A type sheep produce heavier wool in Chokla breed in India.

In Welsh Mountain sheep, WATSON and KHATTAB, (1964), reported that Hb A and AB lambs were slightly superior to Hb B lambs in weight gains up to 8—12 weeks of age, whilst sheep with the A gene produced heavier fleeces. This fleece weight difference was significant in only one year of a five year study. These results indicate that body weight or growth rate would probably not be responsible for fertility differences that may exist between Hb types. LAZOVSKII, (1977), concluded that lambs with Hb B had a significantly higher average birth weight than those with genotype AB, but AB lambs were heavier at weaning in Precoce, Latvian Darkheaded and Romanov sheep in the Soviet Union.

2.1.3.1. Ewe and ram fertility

KING et al., (1958), were the first to investigate the possible relationship between the Hb type and fertility in a large number of Scottish Blackface sheep over a three year period. These characters were studied in association with potassium blood types as described by EVANS, (1954). Considerably diverse results were obtained for the fertility characters studied although Hb types did not differ significantly in these characters. The proportion of lambs weaned to ewes mated was slightly higher for haemoglobin B type ewes. MEYER et al., (1967), obtained similar fertility results in German Blackheaded Mutton ewes.

In a study of four medium Peppin Merino flocks, EVANS and TURNER, (1965), found that Hb A ewes had fewer lambs born and fewer lambs weaned than did AB and B ewes. The slight advantage of the Hb B ewes was associated with either the production or survival of twins. However, MAYO et al., (1970), did not detect any association between fertility and Hb type in the South Australian Merino (of Bungaree type). In one flock, where selection was made on the basis of normal stud classifying methods, the fertility of Hb A ewes was 23,7 per cent higher than that of Hb B ewes, whereas in the other flock, where selection was made on the basis of net merit computed from measured characters, the Hb B ewes were 21,8 per cent more fertile than Hb A ewes. In two North Indian carpet wool breeds, viz. Nali and Lohi, ARORA et al., (1971), concluded that ewe fertility was better in Hb B animals, though not significantly so.

In Bikaneri sheep in India, SETH, (1968), concluded that heterozygous sheep were superior to homozygous sheep. For the homozygous sheep, higher fertility was associated with those of Hb B. In the same breed of sheep, PANT and PANDEY, (1975), reported an association between Hb type and the ovarian response of multiparous ewes towards exogenous gonadotrophins. The ovulation rate of Hb A ewes was unaffected by the administration of pregnant mare serum gonadotrophin (PMSG), whereas that of Hb AB and B ewes responded significantly. The authors suggested that Hb type may provide a simple means of selecting sheep for increased sensitivity to gonadotrophins. HANRAHAN et al., (1976), looked at the effect of haemoglobin type on the response of Finnsheep to PMSG. Although they did not detect any significant relationship between PMSG and the natural ovulation rate, they reported that Hb type AA had a marked effect on the number of corpora lutea after superovulation using 1 500 IU PMSG.

OBST et al., (1971), have suggested that ewes carrying the Hb A gene have a fertility advantage on pastures on Kangaroo Island, which contain legumes with high oestrogen concentrations. The fact that some ewes are capable of maintaining fertility on oestrogenic pasture, (LIGHTFOOT, 1974), supports this hypothesis. However WORTH et al., (1973), did not obtain significant differences in fertility between the Hb types in flocks grazing on oestrogenic pastures for one year, nor over a period of several years.

Information on the performance of sires of different Hb types is limited. In two Indian carpet wool breeds, ARORA et al., (1971), reported that the fertility of Hb B rams (66,4 per cent) significantly exceeded that of Hb AB rams (53,2 per cent). The Hb A sire was not studied. Ram fertility was defined as the lambing percentage of random groups of ewes mated to rams of different Hb types. The only other study comparing sire groups is that of MEYER et al., (1967), who reported a higher fertility in A and AB rams, than in B rams in a German Blackheaded Mutton flock.

2.1.3.2. Lamb mortality

In a study of matings of sires and dams of various Hb types, ARORA et al., (1971) observed fertility in AB × A matings to be the lowest of all. The authors suggested that possibly the A zygotes had a higher embryonic mortality than did zygotes of other Hb types. Support was lent to this interpretation by the results of AB × AB matings which had the second lowest fertility rate. MEYER et al., (1967), reported that among the progeny of AB × AB matings, there were more B animals than A animals. One interpretation of this result is that A zygotes on average had a higher embryonic mortality rate than B zygotes.

While investigating lamb mortality, KING et al., (1958), reported that the mortality rate of lambs born to Hb B ewes was lower than that of lambs born to Hb A ewes, whilst that of lambs born to Hb AB ewes was intermediate. EVANS and TURNER, (1965), indicated that the greater number of young of Hb B ewes may be connected with the survival of lambs from multiple births. ARORA et al., (1971), reported that mortality of lambs born to Hb B rams was less than that of lambs born to the AB rams. The differences were not significant. LASIERRA et al., (1976), working with Aragon sheep in Spain, have reported that lambs of Hb B type had a lower mortality rate than those of Hb AB type. Detailed climatic data were not presented in any of these reports. OBST and EVANS, (1970), reported that under wet, cold conditions, mortality of fine and medium birth coat lambs from Hb A ewes was significantly lower than that of similar birth coat lambs born from Hb B ewes. Evidence indicated that mortality was governed by wind and rain in the first six hours of life, revealing that any advantage conferred on the individual by the A gene was evident very early in life. In their studies on clover disease, WORTH et al., (1973), did not obtain significant relationship between lamb mortality and the Hb type. Similarly, OBST et al., (1974), did not find differences in mortality between the lambs of ewes of the three Hb types. However, these authors found that Se administration to the ewes markedly increased ($P < 0,01$) the mortality of lambs born to the Hb B ewes. In one study (OBST and EVANS, 1970) where micro-climate was monitored, the reverse applied, although birth coat type was a confounding factor. Evidence presented by these authors supports the hypothesis of EVANS et al., (1958 a), that Hb A sheep are better adapted to cold environments. RASMUSEN, (1976), reported that under Illinois conditions, ewes of haemoglobin type A lost a much higher proportion of their lambs than did ewes of types AB or B. The significance of the environment should be recognized in future investigations of this nature.

2.2. Transferrins

2.2.1. Transferrin types in sheep and their distribution

Transferrin is the iron-binding protein of the blood plasma. The physiological function of transferrin is mainly to act as a medium for the distribution of iron, and in addition to act as a small but extremely easily available iron pool (LAURELL, 1961). In many species of mammals it exists in two or more genetically controlled variant forms. Zone electrophoresis in starch gel as introduced by SMITHIES, (1955), and particularly as modified by POULIK, (1957), has proved a powerful technique for the fractionation

of animal serum proteins. The genetic control of the β-globulins, which in animal sera show the most pronounced diversity, has been studied in most species of domestic livestock. In each species so far studied (cattle, horse, pig, sheep) the genetic control of transferrins is governed by a system of multiple autosomal alleles with full expression of each allele in the heterozygote combinations. ASHTON, (1958 a, 1958 b), first demonstrated this to be true in sheep. The number of detectable alleles varies among species and within the species between component breeds. The number of electrophoretically distinguishable protein zones is a species characteristic (starch gel electrophenograms are immediately classifiable according to species) while the presence, even in the homozygotes of multiple transferrin zones apparently under single gene control, poses some interesting considerations of gene protein relationships. However, the physiological significance of the transferrins also raises the question as to whether there are any selective agencies acting on the transferrin genotypes by which polymorphism is maintained. A number of papers have established that the Australian Merino, (ASHTON and FERGUSON, 1963), American, (STORMONT et al., 1968; RASMUSEN, 1976), British, (KHATTAB et al., 1964; RASMUSEN and TUCKER, 1973; COLLIS and MILLSON, 1976; TUCKER, 1976), Egyptian, (NASRAT and OOSTERLEE, 1955), Hungarian (FESÜS and ORBANYI, 1968; FESÜS, 1967, 1970, and 1972), Indian (ARORA and ACHARYA, 1972; SHARMA et al., 1976), Iranian (PASDOR et al., 1976; BUNCH and FOOTE, 1976), Italian (SARTORE, 1964), Norwegian (EFREMOV and BRAEND, 1965), South African (KING and FECHTER, 1967), Spanish (VALLEJO et al., 1975), Rumanian (VICOVAN, 1975), Russian (BUILOU et al., 1975; ALIEU, 1976) and the Turkish breeds (RAHMAN and KONUK, 1977) possess the polymorphism characters.

Family data (ASHTON, 1958 b; KHATTAB et al., 1964; COOPER, 1967; COOPER et al., 1967; RASMUSEN and TUCKER, 1973) agree with the hypothesis that the difference between the variants is controlled by multiple alleles at a single locus. Each allele corresponds to two transferrin proteins, referred to collectively as a zone pair. There appear to be at least nine transferrin zone pairs, or variants, in sheep (OSTERLEE and BOUW, 1967), distinguishable from one another by starch gel electrophoresis. Originally ASHTON (1958 b and 1958 c), using sera from British breeds of sheep and a phosphate continuous buffer system, identified fourteen distinct phenotypes. These were regarded as representing all but one of the fifteen possible types from a five allele system (A, B, C, D, E in decreasing order of electrophoretic mobility). Each allele appeared to produce two zones of differing intensity, the fainter being the leading zone. Later, in a study of Tf types in Australian Merinos, ASHTON and FERGUSON, (1963), reported seven additional alleles designated F, G, H, J, N, K and L, but, surprisingly enough, there seemed to be no evidence for three of the alleles, namely B, D and E, recognized in English breeds of sheep. Furthermore, although Tf^A was encountered in Merinos, Tf^C was extremely rare. STORMONT et al., (1968), were of the opinion that alleles G, N, C and L in the nomenclature of ASHTON and FERGUSON, (1963), are in fact new alleles. Furthermore, they believed that allele L may be the same as the new allele P described by KHATTAB et al, (1964), which in turn may be the same as the new allele Tf^{E2} in their report.

There is some indication from the literature that transferrin types may have an influence on the adaptation of a species to climate. The evidence from other species (e.g. ASHTON, 1959 b) suggested that the frequency of Tf^E within a breed of cattle may reflect the severity of the climate from which they originated.

2.2.2. The relationship between transferrin types and reproductive performance and production characters in sheep

Transferrin types have been reported to have an effect on reproductive performance in cattle (OGDEN, 1960; ASHTON, 1965; ASHTON and FALLON, 1962), pigs (KRISTJANSSON, 1964;

SMITH et al., 1968), mice (ASHTON and DENNIS, 1971), poultry (MORTON et al., 1965) and fish (FUNJINO and KANG, 1968). In sheep, significant deviations from expected numbers in the distribution of transferrin types in populations and in segregating matings have been reported (COOPER, 1967; FESÜS, 1970 and 1972; FESÜS and ORBANYI, 1968; FESÜS and RASMUSEN, 1971; KHATTAB et al., 1964; KING and FECHTER, 1967; STORMONT et al., 1968; RASMUSEN and TUCKER, 1973).

The possible relationships between transferrin types and production or reproduction have so far received little attention. MAYO et al., 1970, examined the reproductive performance and various production characters of Australian Merino ewes. They showed a striking similarity between transferrin phenotype and fertility. Following this, similar research by RASMUSEN and TUCKER, (1973), on four breeds (Finnish Landrace, Clun Forest, Soay and Merino sheep) in England, indicated that, in Finnish Landrace, as a result of matings of sheep homozygous for Tf^C to those heterozygous for Tf^C, there was a significant excess of homozygous male lambs and heterozygous female lambs. They concluded that »that the transferrin types of sire, dam and offspring somehow influence reproductive performance seems to be certain but it seems certain also that the effects are not easily measurable». The situation is still not clear, however, and some conflicting results have been obtained, e.g. ALIEU et al., (1976), working with Tajik sheep in the Soviet Union reported that the frequency of Tf^C gene in infertile ewes was notably higher than in fertile ewes. At this stage, all we can say is that the transferrin type of sheep would appear to be associated with reproductive performance. However, the physiological basis of the transferrin effects remains obscure.

Until recently the association of transferrin types with the mortality rate has not been studied in detail. However, ASHTON, (1959 a), reported that the transferrin genotype of the parents influenced the proportion of genotypes expected from some reciprocal matings and suggested that the asymmetrical segregation ratios were the results of embryonic mortality caused by the incompatibility of a mother and a foetus of different transferrin genotypes.

Transferrin types have, however, been shown to be of considerable importance in production characters. NIX et al., (1968), examined various production characters of Rambouillet, Targhee, Columbia, Lincoln and Suffolk sheep and reported that there was a marked association between transferrin types and birth weight and average daily gains from birth to weaning. Examining weaning weight and greasy fleece weight they stated that there was a relationship but that it was not statistically significant. This association between transferrin type and production character in Indian sheep was later studied by ARORA and ACHARYA, (1972), and they reported significant variations among transferrin types and yearling weight. Similarly, RAHMAN and KNOUK (1977), working with Merino sheep in Turkey reported that transferrin type was associated with the weight gain. In Romanov, Precoce and Latvian Darkheaded sheep in the Soviet Union, LAZOVSKII, (1977), reported that CC had an average fleece weight significantly higher than sheep with genotype AC. In contrast, MAYO et al., (1970), examined various production characters of Australian Merino sheep and none of the characters examined showed any marked relationship with transferrin type. Subsequent research by BUILOU et al., (1975) on Finnsheep, by EROKHIN et al, (1977) on Kuibyshev sheep in the Soviet Union and by PASDAR et al., (1976) on Iranian sheep has confirmed the findings of MAYO et al., (1970). However, despite these conflicting results the transferrins of sheep provide a basis for further study.

2.3. Potassium

2.3.1. Red blood-cell potassium types and their distribution

Most animal cells maintain a high internal potassium and low sodium-ion concentration by means of the activity of the pump in the

membrane which uses energy derived from the hydrolysis of adenosine triphosphate (ATP) to accumulate potassium ions and expel sodium ions (TUCKER, 1971). Consequently the enzyme adenosine triphosphatase (ATPase) is intimately involved in the potassium or sodium pump mechanism.

In 1898, ABDERHALDEN showed that the red cells of sheep, like those of cats and dogs — but unlike those of most other species — have a low concentration of potassium and a high concentration of sodium. Since this early work, several investigators have published a variety of values for red-cell potassium or sodium concentrations in sheep (KERR, 1937; HALLMAN and KARVONEN, 1949; WIDDAS, 1954; DENTON et al., 1951; KARVONEN and LEPPÄNEN, 1952; BERNSTEIN, 1954), but it was EVANS, (1954), who clearly demonstrated that two distinct types could be found in British breeds. He showed that some sheep with high potassium (HK-type) have red-cell potassium values of 80—90 mEq/litre and other sheep with low potassium (LK-type) have 20—30 mEq/litre. The classification based on the concentration of potassium in the red blood cells suggests that there are four types of potassium — the original HK being divided into three sub-types which have been called Ke β, Ke γ and Ke δ and LK being termed as Ke α (KERR, 1937; EVANS, 1957, TANEJA and GHOSH, 1965).

The genetic basis of the red blood cell characteristics has been the subject of intensive research since their discovery. EVANS and KING, (1955); EVANS et al., (1956); and KIDWELL et al., (1959), have established that this difference is controlled genetically, the gene determining LK type apparently being dominant over that determining the HK type. HK sheep are therefore homozygous for the recessive allele (hh) whereas LK animals are homozygous for either the dominant allele (LL) or heterozygous (Lh). The gene responsible for the LK phenotype is not completely dominant because heterozygous LK sheep have slightly higher mean cell potassium values than homozygous LK individuals (EVANS et al., 1956; KIDWELL et al., 1959; SARTORE, 1961; TURNER and KOCH, 1961; MEYER, 1963 a; KHATTAB et al., 1964 a; DASSAT and BERNOCO, 1966; RASMUSEN and HALL, 1966; TANEJA and ABICHANDANI, 1967; BREWER et al., 1968; EAGLETON et al, 1970; TUCKER and ELLORY, 1970; TANEJA, 1973; SINGH et al., 1976 and KRISHNAMURTHY and RATHNASABAPATHY, 1977).

The distribution of potassium types has been determined in many breeds of sheep all over the world: e.g. in England the breeds with the higher proportion of HK are predominant in the mountain and upland regions (EVANS and MOUNIB, 1957; EVANS et al., 1958 a) whereas the Merino inhabiting the arid areas of Australia are exclusively of the LK type. Later work has, however, shown that HK type predominates over LK in desert areas of India (GHOSH et al., 1965; TANEJA, 1972 and 1973; SINGH et al, 1976). If the ecological distribution of blood potassium types as reported by EVANS and MOUNIB, (1957), is taken into consideration, there should have been more of LK than HK in the Indian desert sheep. EVANS et al., (1958 b), also showed that Hb A and HK types were correlated in different breeds. It is apparent from their work that Hb A is, in fact, not always associated with HK type (e.g. HK and Hb B are commonly associated with each other in sheep in India and the Middle East).

2.3.2. Effect of age, sex and breed on potassium levels

Red blood cell potassium in sheep has been shown to be affected by age, sex and breed. HALLMAN and KARVONEN, (1949), found a higher concentration of potassium in the erythrocytes of foetal lambs than in those of rams. On the other hand, KIDWELL et al., (1959), reported that differences in the potassium (K^+) in the blood of sheep of a particular breed were not due to the effect of sex, age nor reproductive status. TURNER and KOCH, (1961); HALL and HUNTER, (1973), reported no difference in the K^+ of rams and ewes. However, EVANS, (1961), found a significantly higher

concentration of potassium in the whole blood of rams compared with that of ewes and thought that steroid hormones might in some way modify the expression of the potassium gene and that the K^+ might be an indirect reflection of steroid levels. WIDDAS, (1954), investigated the effect of the age and revealed a decrease with age in the K^+ of foetal lambs from Welsh Mountain sheep. WRIGHT et al., (1958), estimated sodium and potassium concentrations in the blood of lambs over the period of 12 to 60 days after birth and concluded that with advancing age there is an increase in the sodium content accompanied by a decrease in the potassium content. Similar results were obtained by KOCH and TURNER, (1961). FIELD et al., (1969), and HALL and HUNTER, (1973), noted an irregular effect of age on plasma potassium. Differences in the red cell potassium concentrations of sheep of different breeds, (MEYER, 1963 a), and of strains within a breed, (TURNER and KOCH, 1961), have been described but such a difference was not discovered in the study of HALL and HUNTER, (1973), of four breeds (Blackface, Cheviot, Welsh and their crosses). Environmental influences may, however, produce a variability in (K^+) between animals (DANCEL et al., 1961). HARTMANN, 1977, working in Germany with German Blackheaded Mutton × Finnish Landrace ewes, has reported a change in the distributions of haemoglobins and blood K^+ type by increasing the percentage of Finnish Landrace genes.

2.3.3. The relationship between the red cell potassium and productive/reproductive performance in sheep

Possible relationships between potassium type or red blood cell potassium concentration and production or reproduction has so far received little attention. KING et al., (1958), examined the reproductive performance and a variety of other production characters of Scottish Blackface ewes. None of the characters that they examined showed any significant relationship with potassium type. WATSON and KHATTAB, (1964), reported that LK animals had a marginally better neonatal growth than HK animals, while MEYER et al., (1967), suggested that HK was associated with a reproductive advantage in Germany. TURNER and KOCH, (1961), examined the reproductive efficiency of the LK ewes in Australian Merino and concluded that »there is an indication that ewes with (K^+) values near the mode have better reproductive performance than ewes with values outside the modal class».

Apart from these reports there has been little evidence to suggest that relationships exist between potassium type and reproductive efficiency in the sheep. WATSON and KHATTAB, (1964), looked at the effect of potassium type on birth weight, neonatal weight gain and fleece weight in Welsh Mountain sheep. Although no marked relationships were found, they reported that pheonotypically LK animals had a small but consistent superiority over HK phenotypes in birth weight and daily neonatal weight gain. TANEJA and GHOSH, (1967), investigated body weight and fleece weight in relation to blood potassium types in Marwari sheep in India and their findings revealed that LK animals tended to have higher wool and body weights than HK sheep. In a later study TANEJA et al., (1969), who have shown the frequency of the high potassium HK gene to be associated with differences in wool fibre diameter both between and within breeds, have also suggested that when LK animals of different breeds are compared, there is a positive correlation between fibre diameter and the level of potassium in the erythrocyte. These findings have been confirmed by EVANS et al., (1973), and TANEJA and KHAN, (1974).

2.4. Glutathione

2.4.1. Glutathione types, genetics and distribution in sheep

Glutathione is an essential cellular constituent and is synthesized in erythrocytes from its constituent amino acids, glutamic acid, cysteine and glycine. In most mature mammals GSH-

concentration in the blood is relatively constant, (SRIVASTAVA and BEUTLER, 1969). It has been shown that GSH is involved in protecting haemoglobin against irreversible oxidation denaturation, guarding membrane lipids against peroxidation and shielding essential enzymes against inactivation, (PRINS and LOOS, 1969 and JAFFE, 1970). Recent findings suggest that a major function of glutathione consists in its role as a donor of the γ-glutamyl groups which serve as a carrier in amino acid transport, (MEISTER, 1973).

SMITH and OSBURN, (1967), first reported a deficiency of reduced glutathione (GSH) in the erythrocytes of three sheep in a flock of 104. TUCKER and KILGOUR, (1970), demonstrated that sheep could be classified into two types; high or normal GSH type, with a mean GSH value of 100 mg/dl of erythrocytes and low or deficient types, having a mean GSH value of 30 mg/dl. They stated that in the Finnish Landrace breed, the level of erythrocyte GSH appears to be controlled by a single pair of autosomal alleles, giving rise to two GSH types, GSH-high (GSH^H) and GSH-low (GSH^h), the GSH^H allele being dominant. In a later study, TUCKER and KILGOUR, (1972), using data obtained from Merino × Clun Forest matings, suggested that erythrocyte GSH levels in the Australian Merino are also under genetic control. However, in this case their evidence indicated that the GSH-low gene was dominant. More recently TUCKER et al., (1976), have confirmed the previous findings and when these results were compared with those obtained for Australian Merinos (BOARD et al., 1974) it seems that there is still an ambiguity. BOARD et al., (1974), examined a large number of the Australian Merino sheep and found that their GSH deficiency is similar to that of the »Finn types» in that it is inherited as an autosomal recessive gene.

Several studies have established that glutathione is under genetic control (AGAR et al., 1972; TUCKER and ELLORY, 1971; TUCKER et al., 1973; KALLA and GHOSH, 1975; AGAR, 1975 and KANDASAMY et al., 1976).

In cattle (KUNKEL et al., 1954) and poultry (STUTTS et al., 1956; SABALINA and IOGOV, 1967) erythrocyte GSH concentration has been shown to be highly inheritable, although neither cattle nor poultry have as yet been shown to exhibit an erythrocyte GSH polymorphism similar to that found in sheep. The wide range of erythrocyte GSH concentrations, which are found within both the GSH-high and GSH-low sheep, varies from breed to breed, although the exact mode of inheritance of GSH concentrations remains a subject of controversy.

2.4.2. Red blood cell glutathione in relation to other physiological characters

The GSH-deficient red cells are characterized by having high concentrations of the dibasic amino acids lysine and ornithine and correspondingly lower than normal Na^+ and K^+ levels (ELLORY et al., 1972). The two Finn GSH phenotypes can be identified by a simple screening test which demonstrates the presence or absence of these amino acids, GSH-deficient (low-GSH) cells being amino acid positive (Ly+) and normal (high-GSH) cells showing a virtual absence of lysine and ornithine (Ly—), (ELLORY et al., 1972). Recent work has shown that this GSH deficiency is due to a lack of availability of the GSH-precursor cysteine, resulting from an impaired permeability of the red cell to this and certain other amino acids, including ornithine and lysine, (YOUNG et al., 1975, 1976).

In human beings, deficiency of erythrocytic GSH results in hemolytic anaemia (BOIVIN and GALAND, 1965; PRINS and LOOS, 1969; MINNICH et al., 1971 and KONRAD et al, 1972). Studies reported in the literature indicate that GSH deficiency in sheep erythrocytes does not affect the physiology of these cells (SMITH and OSBURN, 1967; TUCKER and KILGOUR, 1970 and 1972; TUCKER and ELLORY, 1971; AGAR and ROBERTS, 1971; AGAR and SMITH, 1973; SMITH, 1973; SMITH et al, 1974 and TUCKER et al., 1973).

However, significant differences in the activities of both ouabain- sensitive and ouabain-insensitive adenosin triphosphatase, (AGAR et al, 1973), glutathione peroxidase (GP), (AGAR and SMITH, 1973), γ -glutamylcycteine synthetoase (SMITH et al, 1974) and pentose phosphate pathway (PPP) (AGAR and O'SHEA, 1975), have been reported in the erythrocytes of normal and GSH-deficient sheep.

TUCKER and KILGOUR, (1970), reported an association between potassium concentration and reduced glutathione (GSH) level in the erythrocytes in both high potassium (HK) and low potassium (LK) type sheep. AGAR and ROBERTS, (1971), however, could confirm these findings only with regard to the HK animals, no significant relationship being found within the LK group. An interesting speculation made by TUCKER and KILGOUR, (1970), repeated by TUCKER, (1971), envisages that the HK—GSH-low type sheep might in fact be the Ke δ potassium type (a sub-type of HK) sheep, described by EVANS, (1957). In Rajasthan desert sheep in India, KALLA et al., (1972), found no significant correlation between blood potassium and GSH concentrations within any given K—GSH type. According to TUCKER and KILGOUR, (1972) and HOPKINS et al., (1975), there is no difference in (K^+) plus (Na^+) between GSH-high and GSH-low sheep.

The relationship between erythrocyte glutathione level and haematocrit studied by AGAR et al., (1972), revealed that GSH-high (GSH^H) animals have significantly higher haematocrit values. KIDWELL et al, (1958), working with sheep, were unable to find any relationship between these characters.

A negative relationship between haematocrit and GSH level has been reported in man (CERNOCH and MALINSKA, 1966).

Transferrin type has been reported to be associated with glutathione levels in cattle (FOWLE et al., 1967 and NEETHLING and OSTERHOFF, 1968) and in pigeons (BROWN and SHARP, 1970). There is no information available about the relationship between transferrin and glutathione levels in sheep.

2.4.3. The effect of age on reduced glutathione levels

An increase in erythrocyte GSH with age has been reported in man (BERTOLINI et al., 1962 and GOLDSCHMIDT, 1970), rhesus monkey (BROWN et al., 1970), and pigeons (BROWN and SHARP, 1970). However, the relationship between erythrocyte GSH and age in ruminants has been the subject of conflicting reports. REID et al, (1948), reported an increase in erythrocyte GSH with age in cattle and KUNKEL et al., (1954), found no difference in GSH values between calves and adult cattle, while GURTLER et al., (1965), and PODGORSKI and MAJEWSKI, (1969), have reported higher values in calves than in adults. MABON, (1969), found that changes in glutathione concentration were related to feeding efficiency in neonatal calves. In sheep, KIDWELL et al., (1958), and SMITH, (1973), reported no difference between GSH levels of lambs and ewes. In contrast AGAR and ROBERTS, (1971) observed a decrease and then an increase within the first eight weeks of life in the lambs. AGAR et al, (1972) and ATROSHI and ÖSTERBERG, (1979), also found that erythrocyte GSH values rise with increasing age up to 3 or 4 years.

2.4.4. The relationship between GSH levels and production characters

Because erythrocyte GSH types are genetically controlled and the GSH concentration within these types is highly inheritable (BOARD et al., 1974), several investigators have emphasized its relationship to some production traits in animals. For example, erythrocyte GSH has been correlated with adult body size in rabbits, (GREGORY and GOSS, 1933), with growth rate in poultry, (CHARKEY et al., 1965; SABALINA and IOGOV, 1967; MAKRUSHIN, 1968 and OWENS et al., 1970), and with milk yield, growth rate and body size in cattle (KIDWELL et al., 1955; SLEPKOV, 1961; BORISKENKO, 1961). In sheep SALTYKOV, (1956), found a positive correlation between erythrocyte GSH levels and fleece weight. Similarly AGAR et al., (1972), found

that fleece and body weights are positively correlated with erythrocyte GSH levels. In five sheep breeds it reaches a high degree of statistical significance in the GSH^H group, whilst KALLA and GHOSH, (1975) and HOPKINS et al., (1975) reported a negative correlation between wool production and the erythrocyte concentration of reduced glutathione. Both groups found a higher wool production in GSH low-type animals than in GSH-high types. HOPKINS et al., (1975), concluded that selection for GSH-low type sheep may provide a method for manipulating wool production. More recently, KANDASAMY et al., (1976) examined some production characters (e.g. growth rate, weaning weight and fleece weight) of Nilagiri sheep in India. They reported a significant correlation between weaning weight and GSH-low type sheep but were unable to show significant correlation with other growth traits and fleece weight. TUCKER et al., (1976), looked at the effect of glutathione type on lamb mortality in Finn × Merino × pure Finn. They revealed that mortality was significantly higher in GSH-'double-low' lambs from that of high-GSH lambs.

2.5. Conclusions

In conclusion, the important facts emerging from the foregoing review are: (1) There is gene-controlled biochemical diversity in sheep and this diversity, including those examples of it which constitute true polymorphism, probably leads to a slight broadening or narrowing of the range of physiological activity of the specific substance formed and (2) Some of the biochemical parameters have already been shown to be associated — at least in part — with production traits. So far, the practical value of the associations found is perhaps not so great. However, as more evidence is accumulated and several biochemical markers included, this field of study will become more important.

3. PRESENT STUDY

3.1. Materials and methods

The native sheep in Finland is the Northern short-tail which has links with the Romanov breed of Russia and also the sheep of the Orkney and Shetland Islands off Scotland which were once occupied by Scandinavians. In Finland, 95 % of the sheep are 'Finnsheep'. Other breeds which have been introduced for trials are the Texel, the Norwegian Rygja, the Cheviot, Lincoln and the German Blackheaded Mutton sheep. Sheep in Finland have traditionally been suppliers of meat and wool for the families which own them, although ten years ago less than 0,5% of the flocks had around 10 adults in each. There is a need for the development of larger flocks for meat production (MAIJALA, 1969). Improvement and progeny testing have a long history in Finland and systematic recording began in 1918 by the Sheep Breeders' Association; selection for growth rate, prolificacy and milking ability, as well as fleece weight and wool quality has been carried out by this association. Attention is now being paid to muscle development to give the conformation desired in meat sheep. VARO, (1968), demonstrated the existence of many variations in meat characters which could be used in selection work.

The sheep used in the present study come from three regions; Lapland (the North of Finland, the region being one of low winter temperature), Savo (eastern Finland) and Uusimaa in southern Finland. While the survey of blood haemoglobin and transferrin types was carried out on the flocks of all three regions, the population examined consisting of 1 650 adult sheep and lambs, the research into blood glutathione and potassium concentrations was carried out on the flocks

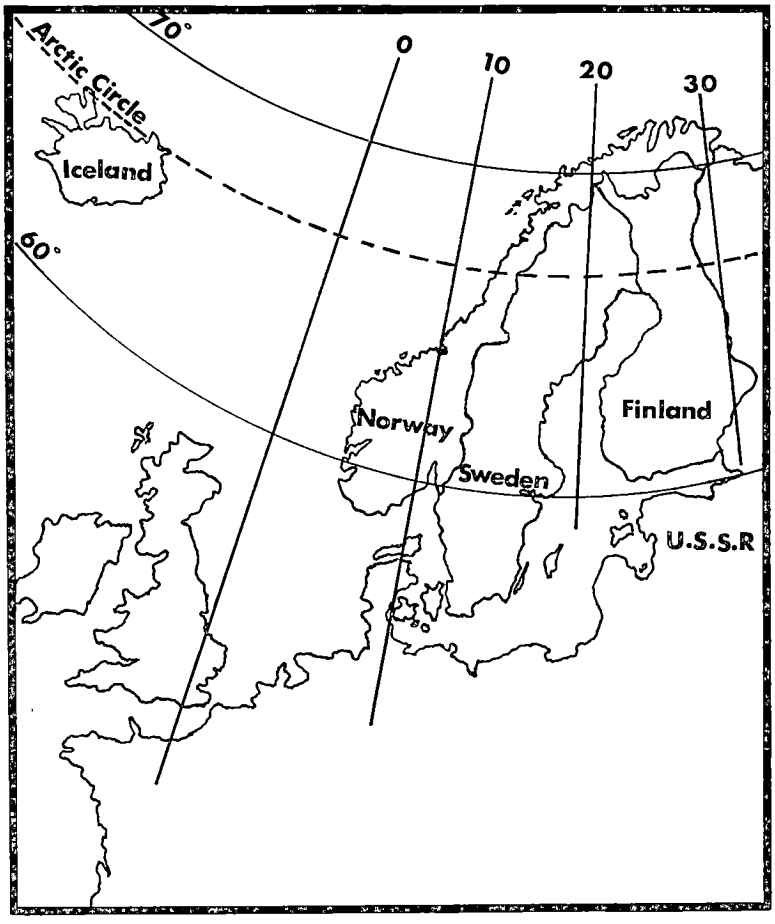


Fig. 1. The geographical location of Finland

of only the last two regions. 760 animals were used in this study. It was not possible to sample the sheep born in the northern region for blood glutathione and potassium, owing to climatic and transportation difficulties. The animals used were rams, ewes and lambs, and at the time of sampling, 1976—78, the animals varied in age from 3 months to 8 years.

3.1.1. Farm environment and management

Finland is situated in northern Europe, lying between the latitudes 60° and 70°N, with approximately a third of its length to the north of the Arctic Circle, (Fig. 1) and the differences in temperature between these two latitudes are considerable. However, sheep are housed in winter and therefore the differences are minimized. The pasture season extends over no more than about five months in the southern region and four months in the northern region. It begins in late May or early June and lasts until September—October and during the rest of the year the sheep are kept indoors and fed on hay, oats and some silage and small quantities of concentrate one month before lambing and during lactation, until the ewes are put out to pasture. The small average flock size has enabled bottle feeding of lambs. The lambs are born indoors during March or April and lactation continues for four to five months, so that by the late summer the lambs have reached live weights of 30—40 kg and are ready for slaughter. The management practice does not differ much from farm to farm. The

recordings concern the autumn weights and annual wool yields of ewes, lambing dates, litter size at birth and weaning, lamb mortality at different ages: still birth, from 0—3 days, 4—14 days, and from 14 days—4 months, ear numbers and sires of lambs, individual weights of lambs at 3 days and 4 months and litter weights at 4 months. In the experimental flocks of the Agriculture Research Centre, individual weights of lambs at birth, 3, 6 and 8 weeks and at 5 months, are also recorded. These measurements were included in the present study.

3.1.2. Determination of haemoglobin types

Blood was taken from the external jugular vein by using (1,20 × 38 mm) gauge bleeding needle, into clean dry 15 × 125 mm test tubes. The anticoagulant used was citrate (2 % sodium citrate plus 0,5 % NaCl). In each case about 10 ml of blood was collected directly into a test tube containing 1 ml of citrate. Blood samples were transported under cool conditions and processed in the laboratory without much loss of time. Zone electrophoresis in starch gel was used in the analysis of haemoglobin phenotypes using the method of BRAEND and EFREMOV, (1964). The erythrocytes were separated from the plasma by centrifugation and the cells washed three times in 0,9 % sodium chloride and hemolyzed with a quantity of water, sufficient to give a haemoglobin concentration of approximately 10 % by volume. Electrophoretic separation was accomplished on an electrophoresis cell by E. Nilson instrument AB-Sweden, using Heto Cooling system at 8°C (Heto, Denmark). The analysis was made in borate buffer pH 8,5 (Tris-lithium hydroxidestric acid). The starch gel was prepared with 32 g of hydrolysed starch (Connaught Laboratories Limited — Canada) in 300 ml of borate buffer. Ten microlitres of each 10 % haemoglobin solution was placed on a Whatman filter paper. Strips were placed in an incision 5 cm from the cathodic end of the gels, having a dimension of 240 × 148 × 6 mm. They had previously been heated to 45°C and poured over the region of the samples, covered with plastic film and left for 12 hours; fifteen samples could be analysed simultaneously. The strips were removed after an electric current had been applied through them at 190 volts for 7 minutes. Electrophoresis was then continued using 190 volts for three hours, until the borate boundary had migrated 12 cm beyond the origin. The gels were sliced using rigid steel pieces and the results were determined by visual examination.

3.1.3. Determination of transferrin types

Blood samples were collected from the external jugular vein and put into clean, dry 15 × 125 mm test tubes to a level of one-half full. A 1,20 × 38 mm bleeding needle was used. The tubes were stopped up with a cork and placed in a horizontal position so that contact occurred between the blood sample and cork. The samples were left at room temperature for one hour to facilitate clotting and then placed in a refrigerator at 5°C to allow clot shrinkage to occur. The tubes were kept in a horizontal position at all times and the following morning the samples were taken out of the refrigerator. The corks were carefully removed from the tubes in order to withdraw the clot adhering to the cork. The fluid remaining was transferred to clean tubes and centrifuged for 5 minutes at 775 *g.* in a refrigerated angle centrifuge. The serum was collected in 2 ml plastic tubes and stored at —20°C. Determination of the serum transferrin phenotypes was made using a modification of the horizontal gel method (GAHNE et al., 1960) described by SMITHIES (1955). The starch gels were prepared from 31 g of hydrolysed starch (Connaught Lab. Canada) in 300 ml of borate buffer of pH 8,0 using the technique outlined by GAHNE et al., (1960). The buffer was prepared by dissolving 11,8 g of boric acid and 0,75 g of lithium hydroxide in 1 000 ml of distilled water, adding 1,6 g citric acid and 4,8 g Tris in 1 000 ml of distilled water until the desired pH was obtained. A slit was made across the gel (previously heated to 45°C and poured over the region of the samples, covered with plastic film and left for at least 12 hours) and partitions in the slit were made with

rigid steel pieces. The samples (approx. 0,05 ml) were inserted on pieces of filter paper. It was possible to insert 17 samples into a gel having dimensions of 240 × 148 × 6 mm. The gels were assembled for electrophoresis using platinum electrodes and potential difference of around 380 V and a current about 4,5 mA applied for 3 hours. At the end of the electrophoresis, the gel was sliced. A 2 mm thick slice in the middle of the gel was stained with a concentrated solution of Amido Black 10 B in methanol water-acetic acid, 50: 50: 10. The transferrin phenotypes were identified by reference samples kindly supplied by Dr. E. M. TUCKER, Institute of Animal Physiology, Cambridge, England.

3.1.4. Determination of potassium

Blood samples were collected from the jugular vein of 760 sheep, using 1,20 × 38 mm bleeding needle and run directly into a plastic test tube containing 0,5 mg of heparin. The whole blood was mixed a hundred parts to one with 0,1 N HCl. Absorbance was measured by the AAS with airacetylene flame (Atomic Absorption Spectrophotometer, Varian Techtron 100) at a wave length of 766,49 nm. The standards were: 0, 3, 5, 6, 7, 9, 10, 15 and 20 mg/l. The absorbance persentages were: 25, 46, 55, 64, 81, 92, 140 and 198 (r = 9,125). From the standard curve the regression coefficient was calculated. The absorption of the samples was divided by the regression coefficient to get the amount of potassium in the whole blood, mg/l. As the sample was diluted 1: 100, the figure is multiplied by 100 to get the exact figure and when this is divided by the haemotocrit value of the sample one gets the amount of potassium in the red blood cells mg/l. To get the figure in m. equiv./l it must be divided by the atomic weight of the potassium (39,1).

3.1.5. Determination of glutathione

1. **Precipitation solution:** 1,67 g glacial methaphosphoric acid (a mixture of HPO_3 and $NaPO_3$), 0,2 g disodium or dipotassium ethylene diamine tetra acetic acid (EDTA) and 30 g sodium chloride were dissolved in 100 ml of distilled water, as this solution can be stored for up to three weeks when kept at 4°C. The fine precipitation that may appear is probably EDTA and does not matter. We did not deem it necessary to add EDTA but added it to the solution to avoid those difficulties that might arise if the water contains large amounts of metallic ions.

2. **Phosphate solution:** A solution of 0,3 M Na_2HPO_4 was prepared and added to distilled water and this solution could be used until mould was formed. If crystals were formed during storage (at 4°C) they could be dissolved by heating.

3. **DTNB-reagent:** 40 mg 5,5' dithiobis (2-nitro benzoic acid) was dissolved into 100 ml of a 1 % sodium citrate solution. Sodium citrate was chosen because its pH value is suitable from the point of view of the solubility of the reagent as well as of its stability. A phosphate buffer of pH 7—8 can also be used. The DTNB reagent can be used for at least 13 weeks when kept in a refrigerator.

4. **Method:** GSH levels in whole blood were determined spectrophotometrically according to the method of BEUTLER et al., 1963, within 24 hours of collection. To 0,2 ml whole blood, 1,8 ml of distilled water was added and 3 ml of the precipitation solution was mixed with the hemolysate. The amount of the precipitation solution is not decisive. The mixture was left for about five minutes and then filtered. 2 ml of the filtrate was added to a cuvette (25 × 105 mm) with 8 ml of phosphate solution. 1 ml of DTNB solution was added and the reagent blank prepared from 8 ml phosphate solution, 2 ml diluted precipitation solution (3 parts + 2 parts distilled water) and 1 ml of DTNB-reagent. The absorption was measured at 412 nm with a spectrophotometer.

5. **Standardization:** The purity of the glutathione was measured iodometrically, (WOODWARD and FRY, 1932). The purity was about 102 %, the surplus depended on the cysteine which was an impurity.

Region	No. of sheep sampled
North	567
East	541
South	459
Total	1,567

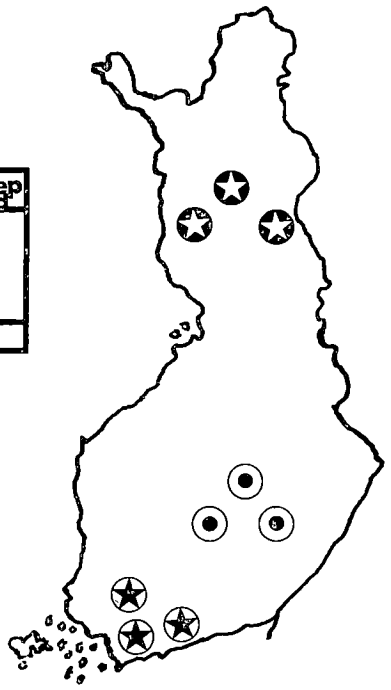


Fig. 2. Distribution of blood samples of sheep with complete records of different regions in Finland.

6. **Determination of glutathione:** The standards of the glutathione were expressed in mM. The figure was multiplied by the molecular weight of glutathione (307,33) in order to get it in mg/l; apart from this, the figure was obtained in the same way as that for potassium.

7. **Haematocrit:** The haematocrit value of the blood samples (i.e. the percentage of red blood cells) was estimated by using a micro haematocrit centrifuge (Christ-Heraeus).

3.1.6. Statistical analysis

The blood characters and the measurements of each animal were coded, transcribed on to punched cards and run on computer (Hewlett Packard 21-MX type). Distribution of the animals over the various regions is shown in Fig. 2. In all the samples measured there was some loss of information. No attempt was made to estimate missing values. A nested or hierarchical analysis of variance with unequal subclass numbers was chosen as the method of analysis (SOKAL & ROHLF, 1969) in order to determine the relative importance of the blood characters of the ewe, ram, mating type and lamb in the variation of production traits, viz. the number of lambs born and weaned, lamb mortality rate, including stillborns, ewe body and wool weights and lamb weights at different ages. There were several reasons for placing the main emphasis on this analysis. The main reason for confining the analysis to differences within progeny groups is a genetic one: if there is a concentration of the blood lines within the breed, associations between the blood characters of a sire and the performance of its descendants can be found. An analysis made within progeny groups should be fairly free of chance associations. Secondly there were three regions with unequal numbers of observations and several variables were to be tested at the same time.

The models on which a nested anova was based included the effects of region, farm, sire, the age of the ewe and the sex of the lamb and the blood characters studied, as follows:

1. $Y_{ijklmn} = \mu + a_i + A_{ij} + B_{ijk} + b(X_{ijklmn} - \overline{X}) + C_{ijkl} + D_{ijklm} + \varepsilon_{ijklmn}$

Where

Y_{ijklmn} is the nth observations within the mth blood type within the lth sex within the kth sire within the jth farm within the ith region

μ is the parametric mean of the population

a_i is the effect of the ith region

A_{ij} is the effect of the jth farm within the ith region

B_{ijk} is the effect of the kth sire within the jth farm within the ith region

b is the regression coefficient on age

X_{ijklmn} is the age

$\overline{X}$ is the mean age

C_{ijkl} is the effect of the lth sex within the kth sire within the jth farm within the ith region

D_{ijklm} is the effect of the mth blood type within the lth sex within the kth sire within jth farm within the ith region

ε_{ijklmn} is the error term of the nth observations within the mth blood type within the lth sex within the kth sire within the jth farm within the ith region

2. $Y_{ijkl} = \mu + a_i + B_{ij} + C_{ijk} + \varepsilon_{ijkl}$

Where

Y_{ijkl} is the lth observations in the kth blood type within the jth sire within the ith farm

μ is the parametric mean of the population

a_i is the effect of the ith region, farm, or sire

B_{ij} is the effect of the jth sire within the ith farm

C_{ijk} is the effect of the kth blood type within the jth sire within the ith farm

ε_{ijkl} is the error term of the lth observations in the kth blood type within the jth sire within the ith farm

3. The tabulation of the results is as follows:

Source	MS	Exp. MS
Between sires	MS_s	$\sigma^2 + k_2\ \sigma^2_d + k_3\sigma^2_s$
Between dams	MS_d	$\sigma^2_\varepsilon + k_1\sigma^2_d$
Within dams	MS_ε	σ^2_ε
Total		$\sigma^2_\varepsilon + \sigma^2_d + \sigma^2_s$

where: σ^2_ε is the component within group, σ^2_d the component between dams and σ^2_s is the component between sires. Negative variance components were considered as zeros in computing the percentages except in the pooled results. In cases where significant differences between the blood parameters were found, the direction and size of the effects were computed according to the formula:

$$\overline{D} = \frac{\Sigma wd}{\Sigma w}$$

where $w = \frac{n_1 n_2}{n_1 + n_2}$, n_1 and n_2 are the number of animals in section and $d = X_1 - \overline{X}_2$ within each sire (NEIMANN-SØRENSEN and ROBERTSON, 1961). The standard error of this difference was computed according to the formula:

$$\sqrt{\frac{\sigma w^2}{\Sigma w}}$$

where $\sigma\ w^2$ means the total variance within sections of animal groups (FALCONER 1963). Because of the age variations in the animals, partial correlation for the different blood characters corrected for age were used (SNEDECOR & COCHRAN, 1967).

Genotype and gene frequencies were estimated by the direct counting methods (RACE & SANGER, 1950). In cases where the frequencies of these types were compared, the standard errors were computed according to the formula:

$$s = \sqrt{\frac{1 - q_a^2}{4n}}$$

where q_a is the relative frequency of the recessive gene and n is the number of animals (COTTERMAN, 1954). In mating between LK phenotypes the theoretical proportion of recessive HK among their offspring is:

$$\frac{1}{4}\left(\frac{2pq}{p^2 + 2pq}\right) = \left(\frac{q}{1 + q}\right)^2$$

where the frequency of $K^L = p$ and $K^H = q$. Similarly, in matings where one parent is dominant and the other recessive (LK × HK), the

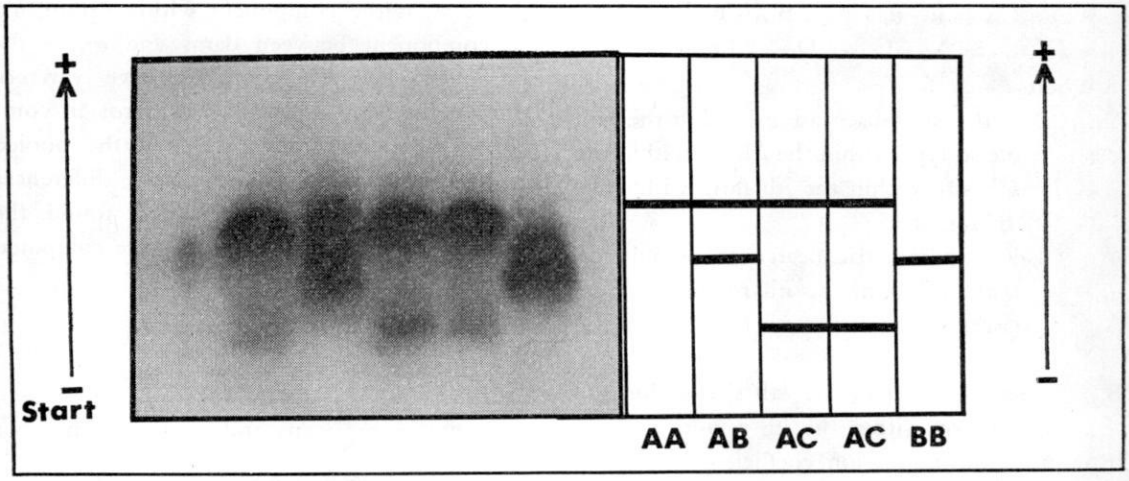


Fig. 3. A photograph of the haemoglobin types described.
The schematic drawing gives the interpretation of the patterns presented by the haemoglobin types.

expected proportion of the recessive (HK) amongst offspring will be $\frac{1}{2}$ when all dominant parents are heterozygous ($K^L K^H$). The expected proportion of the recessive amongst offspring from LK × HK mating is then:

$$\frac{1}{2}\left(\frac{2pq}{p^2 + 2pq}\right) = \frac{q}{1 + q}$$

The segregation pattern and departure from genetic equilibrium was tested by means of a chi-square test (RACE & SANGER, 1950). Because of insufficient numbers in some of the cells, the analysis was generally confined to totals within each of the groups. Occasionally numbers were still limited and the probabilities given should thus be considered in the light of these limitations.

3.2. Results

3.2.1. Haemoglobin

3.2.1.1. Haemoglobin types

Three different haemoglobin phenotypes determined by the two alleles Hb^A and Hb^B were observed after starch-gel electrophoresis according to their mobilities (Figure 3). The fast moving one was designated Hb A, the slow moving one Hb B. Individual animals possessed either one or both the haemoglobins. A third haemoglobin was observed in one ewe and in one of her four lambs, and it appeared as a band, having a rate of migration on starch gel markedly slower than that of the B band. This special band was of approximately the same strength as the A band and has been named C (ATROSHI et al., 1979).

3.2.1.2. Distribution of haemoglobin types

The gene frequencies for haemoglobin types according to geographical distribution are listed in Table 1 and further illustrated in Figure 4. The gene frequencies are obtained by applying the formula first given by WIENER and VAISBERG (1931), which amounts to a direct counting of the two genes. The probability that an animal has a haemoglobin AA phenotype is:

$$\frac{\text{AA phenotype}}{\text{Total phenotype}}$$

$$\text{Gene A} = \text{the probability of A} + \frac{\text{probability of AB}}{2}$$

$$\text{Gene B} = \text{the probability of B} + \frac{\text{probability of AB}}{2}$$

Table 1. Frequency distribution of haemoglobin phenotypes and the gene frequencies of haemoglobin A and B in different regions.

Region	No. of animals	Haemoglobin phenotypes %			Gene frequency		Latitude	Meters above the sea level
		A	AB	B	Hb^A	Hb^B		
North	567	40,56	45,86	13,58	0,635	0,365	68°	150
East	541	64,33	32,53	3,14	0,806	0,194	62°	100
South	459	70,37	23,09	6,54	0,819	0,181	60°	45
Total	1 567	57,50	34,59	7,91	0,748	0,252		

Animals of Hb A type were predominant and the frequency of Hb^A allele in Finnsheep was high (0,748), while that of the allele Hb^B was low (0,252). Altitudes and latitudes are also given in Table 1. There is considerable variation in the frequency of the two alleles between groups born in different regions. Most interesting may be the frequency of Hb^A and Hb^B in the northern region, where sheep live at rather high altitudes, different latitudes and in very cold weather. There the frequency of Hb A was lower than anywhere else (0,635 vs 0,815 in the eastern and southern regions, $\chi^2 = 3{,}490$, 2df, $0{,}2 > P > 0{,}1$) and the frequency of Hb B was higher than anywhere else (0,365 vs 0,188 in the eastern and southern regions, $\chi^2 = 12, 243$, 2df, $0{,}1 > P > 0{,}001$).

Table 2 summarizes the family data in the haemoglobin types and a typical segregation pattern can be observed. Offspring of AA type are not produced if one of the parents is of B type, and BB offspring are not produced if one of the parents is of A type. A × A mating produce only AA offspring, whereas AB × AB matings can produce all three types. However, the two BB offspring from AA × BB matings are unexpected from such a mating and may be attributed to erroneous identity of the progeny. There was an excess of B type offspring from AB × BB matings ($\chi^2 = 8{,}327$, 1 df, $P < 0{,}01$).

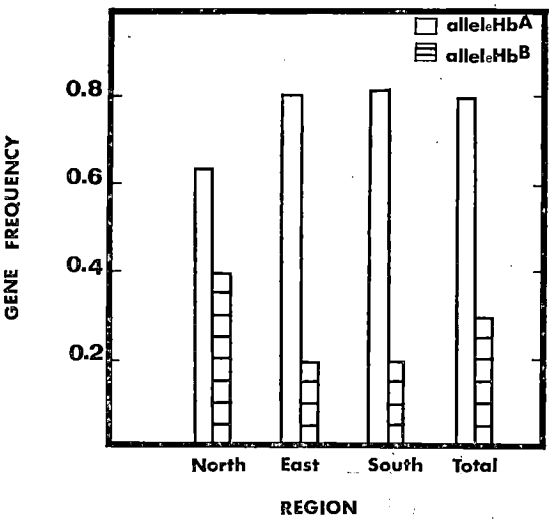


Fig. 4. The frequency of alleles Hb^A, and Hb^B of of Finnsheep in different regions.

Table 2. Distribution of haemoglobin phenotypes in the offspring from nine different matings.

Mating type Ram × Ewe	Number of matings	Distribution of phenotypes						Total	x^2
		Hb AA		Hb AB		Hb BB			
		obs.	exp.	obs.	exp.	obs.	exp.		
AA × AA	180	404	403,5	—	—	—	—	404	0,000
AA × AB	103	76	77,0	60	59,25	—	—	103	0,022
AA × BB	34	—	—	23	21,50	2	0,00	25	0,105
AB × AA	94	49	45,0	34	32,75	—	—	83	0,403
AB × AB	102	25	23,5	53	49,25	12	14,00	90	0,667
AB × BB	38	—	—	16	13,75	20	10,75	36	8,327
BB × AA	12	—	—	85	85,00	—	—	85	0,000
BB × AB	23	—	—	22	17,50	18	14,75	40	1,873
BB × BB	16	—	—	—	—	16	16,00	16	0,000

Table 3. Test of genetic equilibrium for haemoglobin types of sheep in different regions.

Region	No. of animals	Haemoglobin phenotypes						Gene frequency		x^2 (number in each class)
		A		AB		B		Hb^A	Hb^B	
		obs.	exp.	obs.	exp.	obs.	exp.			
N. Finland .	567	230	228,56	260	262,86	77	75,58	0,635	0,365	0,067 NS
E. Finland .	541	348	351,41	176	169,22	17	20,37	0,806	0,194	0,862 NS
S. Finland .	459	323	307,88	106	127,00	30	24,04	0,819	0,181	5,693 (0,01 < P < 0,05)

This may be due to the environmental effects and could be one of the reasons for the higher gene frequency of Hb B in the northern region. The findings are consistent with the hypothesis that haemoglobin types are genetically determined by two alleles each responsible for the formation of one kind of haemoglobin.

Assuming random mating and no differential selection, one can calculate from the Hardy-Weinberg equation the expected proportion of the three phenotypes in the total population.

Table 3 indicates that the observed genotypic number of northern and eastern animals of the three haemoglobin types was not significantly different from the expected number on the basis of the Hardy-Weinberg equilibrium, and so a fairly good agreement was obtained. However, the animals from southern Finland show a departure from the expectation ($\chi^2 = 5{,}693$; $0{,}01 < P < 0{,}05$), this departure is due mostly to a deficiency of heterozygotes.

3.2.1.3. Reproductive performance

The mean values with standard errors for various measurements of reproductive performance, e.g. the number of lambs born and weaned and lamb mortality, according to the haemoglobin phenotype of the ewe, ram and lamb are given in Tables 4—11 and are further illustrated in Figures 5—7. The number of lambs born and weaned from both known parents and for the three regions per ewe put to the ram, was:

Table 4. Reproductive and productive performance of ewes of different haemoglobin types in different regions.

Regions	Ewe Hb type	No. of ewes	Body weight kg	Wool weight kg	Litter size	No. of lambs weaned	4-month litter weight
			$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
North ...	AA	93	57,70±1,28†	2,20±0,10	2,7±0,09	2,4±0,08	63,14±2,05
	AB	105	51,63±1,52	2,11±0,08	2,5±0,11	2,2±0,10	57,69±2,43
	BB	40	54,15±2,45	2,00±0,10	2,5±0,13	2,2±0,12	59,35±3,29
East	AA	117	57,26±0,99	2,53±0,06	3,1±0,10	2,5±0,09	68,30±2,32
	AB	79	52,91±1,35	2,63±0,07	3,0±0,11	2,5±0,06	66,19±2,40
	BB	4	54,61±1,27	2,50±0,10	3,0±0,17	2,8±0,15	66,01±2,31
South ...	AA	113	68,51±1,63††	2,97±0,08†	2,7±0,10	2,2±0,09	67,30±2,24††
	AB	53	66,79±1,45	2,56±0,11	2,8±0,15	2,4±0,12	66,02±3,11
	BB	10	58,90±2,06	2,27±0,09	2,3±0,25	1,6±0,22	41,20±3,46
Total	AA	323	61,74±0,69	2,61±0,25†	2,8±0,06	2,3±0,05	66,73±1,30
	AB	237	55,79±0,95	2,40±0,05	2,7±0,07	2,3±0,06	62,66±1,53
	BB	54	55,90±1,92	2,06±0,08	2,4±0,12	2,1±0,15†	55,86±2,05

† significant at 5 % level.
†† significant at 1 % level.

The sign of significance (†) indicates that in a certain region concerning a certain production/reproduction trait, a certain blood type differs significantly from another blood type (or several other blood types); the text explains which type it is different from.

Table 5. Reproductive performance and production characters of different haemoglobin mating types.

Mating type	No. of sires	No. of ewes	No. of lambs	Litter size	Weaned	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	4-month litter weight.	5-month weight
Sire × Dam				$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
AA × AA ..	10	177	506	3,1 ±0,05	2,6 ±0,04	2,68 ±0,03	3,51 ±0,04	6,53 ±0,07	11,01 ±0,11	14,13 ±0,14	27,67 ±0,29	70,74 ±0,98	32,05 ±0,32
AA × AB ..	6	93	280	3,2 ±0,07	2,6 ±0,07	2,61 ±0,04	3,18 ±0,05	6,48 ±0,08	10,81 ±0,14	13,71 ±0,17	27,03 ±0,39	70,85 ±1,64	30,47 ±0,45
AA × BB ..	3	12	29	2,7 ±0,14	1,0 ±0,01	2,82 ±0,07	3,26 ±0,10	6,58 ±0,35	12,12 ±0,52	15,62 ±0,65	30,23 ±1,19	59,55 ±2,01	33,55 ±1,74
AB × AA ..	5	101	272	3,0 ±0,05	2,5 ±0,04	3,50 ±0,01	3,59 ±0,05	6,52 ±0,26	12,02 ±0,15	15,51 ±0,54	32,00 ±0,38†	74,67 ±1,63	33,54 ±1,74
AB × AB ..	5	100	255	3,1 ±0,07	2,6 ±0,06	3,01 ±0,03	3,28 ±0,05	6,48 ±0,31	10,91 ±0,15	13,51 ±0,16	27,52 ±0,18	69,24 ±1,58	29,45 ±0,39
AB × BB ..	2	30	77	2,8 ±0,08	2,3 ±0,09	2,51 ±0,05	3,16 ±0,10	6,33 ±0,15	10,72 ±0,15	13,65 ±0,15	28,03 ±0,51	59,86 ±1,72	30,27 ±0,53
BB × AA ..	2	34	101	3,3 ±0,20†	3,0 ±0,12	2,59 ±0,05	3,16 ±0,06	6,38 ±0,13	11,01 ±0,21	14,82 ±0,26	27,85 ±0,58	72,22 ±2,71	33,52 ±0,61
BB × AB ..	2	36	94	3,0 ±0,11	2,6 ±0,12	2,65 ±0,05	2,99 ±0,06	6,70 ±0,12	12,23 ±0,29	15,16 ±0,25	28,12 ±0,71	70,31 ±2,46	33,59 ±0,80
BB × BB ..	1	9	19	2,6 ±0,23	2,3 ±0,25	2,67 ±0,06	3,02 ±0,15	6,37 ±0,31	10,91 ±0,18	12,88 ±0,16	26,36 ±0,35	61,27 ±2,65	29,09 ±1,72

† significant at 5 % level.

AA ewes gave 2,75 lambs born, 2,30 lambs weaned, AB ewes gave 2,65 lambs born, 2,25 lambs weaned and BB ewes gave 2,40 lambs born, 2,10 lambs weaned.

These differences were not significant for AA and AB ewes, but it was found that BB ewes had a marked effect on the number of lambs weaned ($P < 0,05$). There were differences between the three phenotypes of ewes within each region and between regions. In most cases AA ewes were better than both AB and BB for number of lambs born, and BB ewes did better than AA and AB ewes for number of lambs weaned, but for lambs born there was no significant difference. In all regions ewes of AA type were found to produce the biggest litters.

Table 5 shows the number of lambs born and weaned per ewe mated from each mating type. BB ♂ × AA ♀ gave the best figure for both lambs born and weaned, but AB ewes did better on average than both homozygotes, giving +0,183 more lambs born ($P < 0,05$) and +0,083 more lambs weaned than the average values of the two homozygotes. Table 6 and Figure 5 show the distribution of litter sizes, AB ewes having larger litters than AA and BB ewes, but the cases of barren ewes were more frequent among AA and AB ewes compared to BB ewes. AA and AB ewes did not appear to differ very much in reproductive performance. In AA and AB ewes the highest percentage of lambs were born as triplets ($P < 0,05$) and in BB ewes the largest percentage of lambs born were as twins. AA ewes mated to AB rams had large litters. The litter size from AA ♂ × AA ♀ and AA ♂ × AB ♀ were similar. The highest percentage of lambs born as quadruplets resulted from AA ♂ × AA ♀, AB ♂ × AB ♀ and BB ♂ × AB ♀ matings. AA ♂ × AA ♀ matings produced a high number of quintuplets. The lowest proportion of singles were among AA ♂ × BB ♀ and AB ♂ × AB ♀ matings.

Looking at the performance of rams (Table 8) we see that in the northern and eastern regions, homozygous rams were better than heterozygous rams, giving + 0,40 and + 0,45 more lambs born respectively. These differences were not

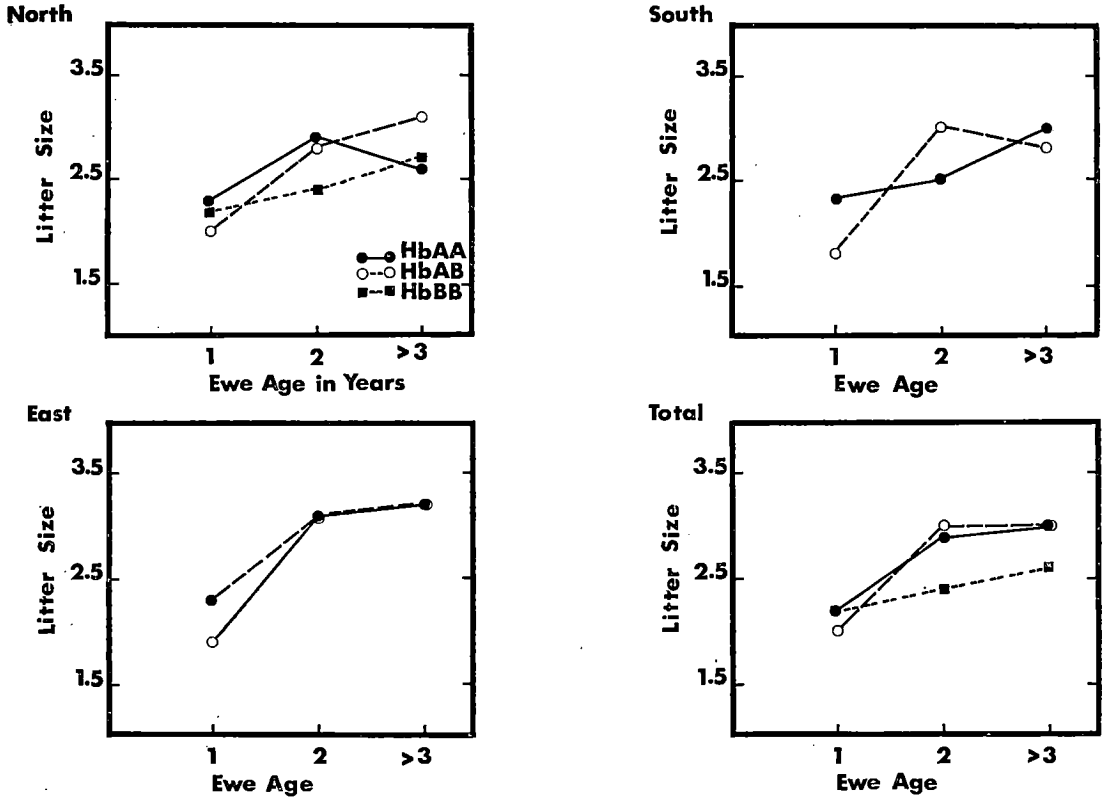


Fig. 5. The relationship between age of ewe and litter size according to ewe haemoglobin type in different regions.

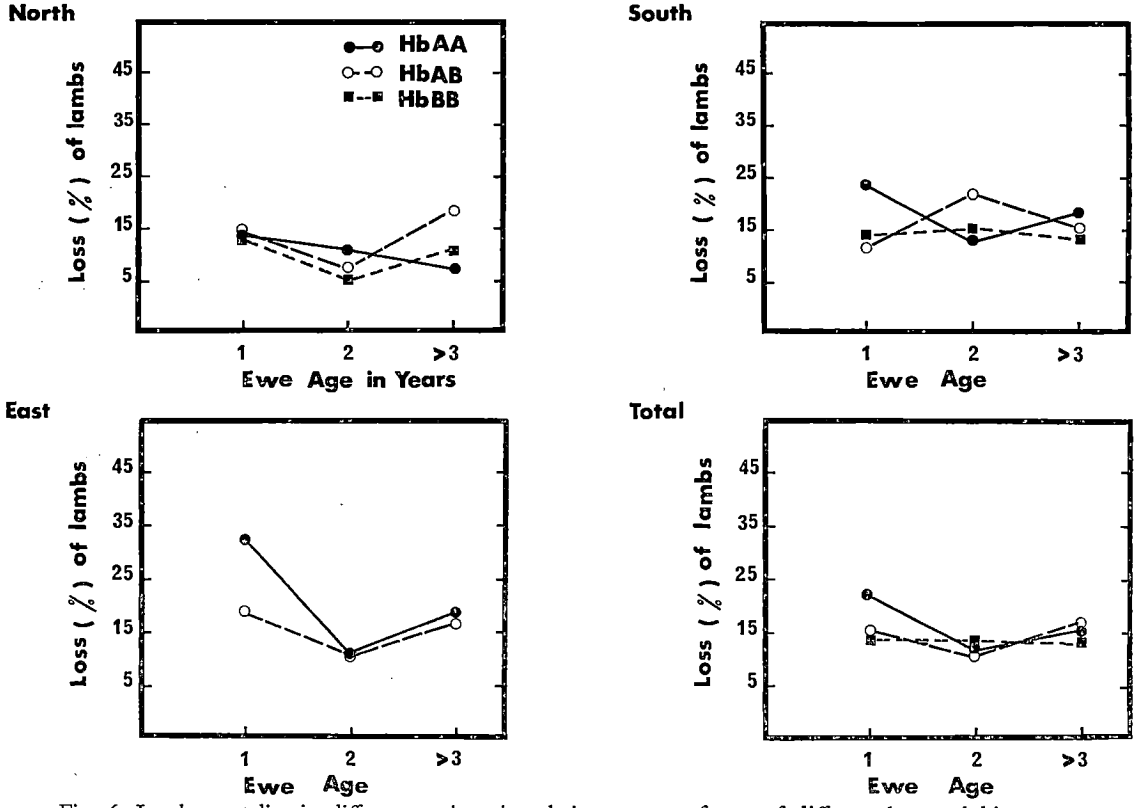


Fig. 6. Lamb mortality in different regions in relation to age of ewe of different haemoglobin types.

Table 6. Reproductive performance of different mating types and of ewes of different haemoglobin types.

Mating type Sire × Dam	No. of ewes	Total Number of lambs per litter							
		0	1	2	3	4	5	6	7
AA × AA	180	4	19	54	59	31	15	0	0
AA × AB	103	3	6	33	46	12	4	0	0
AA × BB	34	0	1	11	12	8	2	0	0
AB × AA	94	4	6	29	38	11	5	2	1
AB × AB	102	4	12	36	31	17	3	2	0
AB × BB	38	1	4	15	12	4	2	0	0
BB × AA	12	2	1	5	5	1	0	0	0
BB × AB	23	3	1	9	8	4	0	0	0
BB × BB	16	0	4	6	6	0	0	0	0
Dam Hb type									
AA	323	10	26	98	116	52	21	0	0
AB	240	10	22	79	82	32	10	4	1
BB	52	1	6	21	19	5	0	0	0

0 = barren ewes.

significant. However, AB rams did better in the southern region giving + 0,30 more lambs than did AA rams and + 0,80 more lambs than did BB rams ($P < 0,05$). The number of lambs weaned was lower for the offspring of the two homozygotes than that of AB rams in the northern and eastern regions. The figures was + 0,25 more lambs weaned. In the southern region, AB rams had 0,5 % fewer lambs weaned than the two homozygotes. The difference was significant at the 0,05 level.

3.2.1.3.1. Lamb mortality

Mortality of lambs from birth to 3 days, 4 to 14 days and 14 days to 4 months is shown in Tables 9 and 11 and correspondingly in Figures 6 and 7. Lamb mortality refers to stillborn, dead and lost lambs (fate unknown). Looking at the proportion within each of these percentages for different haemoglobin types in Table 9, it appears that loss of AA phenotypes is higher than that of BB phenotypes (the differences were significant at the 0,05 level). The general level of mortality and the mortality of different haemoglobin types varies considerably from region to region. Table 10 shows a more detailed examination of the loss of phenotypes and of the age of ewe in the three regions.

Loss of AA is about twice as high for ewe lambs as for older AA ewes (22,3 % vs 11,1 %) but this pattern does not apply to AB and BB phenotypes. Considering stillborn lambs, we again see that AA phenotypes have the highest mortality among ewe lambs, which, however, declines from 12,4 % to 6,1 %, as the age of ewe increases from one year to two years. In general, the percentage of stillborn (losses) was 1,3 %-units higher among homozygous ewes than among heterozygous ewes. Looking at the percentage of lambs which died at different ages one can see that AA and AB ewes suffered greater losses (nearly 2 %) than BB ewes; these differences were significant at 0,05 level.

Table 9 shows lamb mortality according to sex, for different phenotypes in the three regions. The following can be seen: Percentage of losses in AA ewes was 6,1 %-units higher for female than male lambs, the differences in AA ewes not being significant. In BB ewes there were no differences between the percentages of dead male and female lambs.

Regarding the haemoglobin types of the sire (Table 11), loss of the AA phenotype was higher than for AB and BB phenotypes and there was a large variation from region to region ($P < 0,01$). The proportion of stillborn lambs was higher among the homozygous rams than

Table 7. Reproductive performance and production characters of ewes of different age and phenotype, according to region.

Region	Ewe age	Ewe Hb type	No. of ewes	Body weight	Wool weight	Litter size	Weaned	No. of lambs	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
				$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE		$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE	$\bar{x}$ ± SE
		AA	16	41,91±1,12	2,29±0,22	2,3±0,22	2,0±0,16	37	—	3,14±0,19†	—	—	—	28,20±0,75	—
	1 Yr.	AB	42	35,89±1,23	1,97±0,15	2,0±0,10	1,7±0,10	77	—	2,93±0,06	—	—	—	26,76±0,62	—
		BB	14	39,46±1,73	1,78±0,19	2,2±0,19	1,9±0,13	31	—	2,88±0,08	—	—	—	24,60±0,82	—
		AA	33	56,92±1,60	2,15±0,15	2,9±0,18	2,6±0,19	92	—	3,36±0,09	—	—	—	31,56±0,65	—
North	2 Yr.	AB	28	59,44±1,83	2,15±0,15	2,8±0,25	2,6±0,20	79	—	3,30±0,08	—	—	—	31,78±0,53	—
		BB	8	59,00±1,80	2,80±0,05	2,4±0,26	2,3±0,25	19	—	3,35±0,20	—	—	—	27,33±0,98	—
		AA	44	63,94±1,59	2,20±0,16	2,6±0,11	2,4±0,10	116	—	3,67±0,06	—	—	—	32,47±0,54	—
	3 Yr.	AB	38	65,61±1,23	2,25±0,10	3,1±0,21	2,5±0,20	108	—	3,45±0,07	—	—	—	32,19±0,44	—
		BB	18	68,46±1,10	1,95±0,12	2,7±0,20	2,5±0,22	46	—	3,46±0,10	—	—	—	30,28±1,03	—
		AA	14	42,46±1,87	2,54±0,21	1,9±0,23	1,3±0,20	25	2,77±0,13	3,30±0,15†	7,55±0,33	12,51±0,49†	15,63±0,56	26,12±1,10	32,97±1,31
	1 Yr.	AB	19	44,56±1,94	2,66±0,11	2,3±0,16	1,8±0,19	36	2,46±0,12	2,88±0,13	6,78±0,19	11,69±0,41	13,98±0,40	24,05±0,88	30,69±1,15
East	2 Yr.	AA	21	47,13±1,67	2,14±0,13	3,1±0,20	2,8±0,19	62	2,68±0,38	2,89±0,08	6,42±0,17	10,71±0,31	13,64±0,39	25,23±0,86	31,70±0,97
		AB	24	47,26±1,54	2,49±0,17	3,1±0,15	2,8±0,16	74	2,64±0,06	2,66±0,07	6,48±0,15	10,79±0,24	13,71±0,30	25,16±0,83	30,64±0,91
	3 Yr.	AA	82	62,53±0,77	2,63±0,06	3,2±0,11	2,6±0,11	248	2,65±0,04	3,38±0,05	6,41±0,09	10,90±0,16	14,22±0,19	26,72±0,39	32,41±0,44
		AB	36	61,57±1,77	2,71±0,10	3,2±0,17	2,7±0,16	107	2,67±0,05	3,30±0,07	6,41±0,15	10,93±0,26	14,17±0,33	26,36±0,71	31,51±0,76
	1 Yr.	AA	13	55,08±1,07	2,00±0,06	2,3±0,21	1,9±0,19	27	—	3,19±0,16	—	—	— —	26,64±0,83	—
		AB	6	54,33±1,65	1,92±0,17	1,8±0,30	1,7±0,21	11	—	3,12±0,27	—	—	— —	26,27±0,99	—
South	2 Yr.	AA	17	63,12±1,31	3,11±0,10	2,5±0,17	2,4±0,17	43	—	3,90±0,14	—	—	—	27,95±0,82††	—
		AB	5	61,00±1,05	2,24±0,23	3,0±0,31	2,4±0,24	15	—	2,59±0,10	—	—	—	23,67±1,07	—
		AA	30	69,79±1,31	2,87±0,09	3,0±0,22	2,6±0,19	87	—	3,91±0,15†	—	—	—	27,31±0,60	—
	3 Yr.	AB	23	64,61±1,78	2,39±0,17	2,8±0,21	2,7±0,17	65	—	3,05±0,12	—	—	—	25,40±0,68	—
		BB	7	61,86±1,12	2,35±0,11	2,3±0,42	1,7±0,27	16	—	2,82±0,19	—	—	—	25,00±1,50	—

† significant at 5 % level.
†† significant at 1 % level.

Table 8. Reproductive performance and production characters of rams of different phenotypes in different region.

Region	Ram Hb type	No. of rams	No. of lambs	Litter size	Weaned	Birth weight kg	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	4-month litter wt.	5-month weight
				$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
North	AA	5	225	3,2 ±0,09	2,4 ±0,07	—	3,26 ±0,04	—	—	—	31,14 ±0,36	67,59 ±2,06	—
	AB	5	284	2,8 ±0,05	2,5 ±0,05	—	3,52 ±0,05	—	—	—	30,71 ±0,34	64,78 ±1,35	—
	BB	3	96	3,2 ±0,12	2,9 ±0,14	—	3,14 ±0,07	—	—	—	30,79 ±0,65	72,30 ±2,03	—
East	AA	5	346	3,5 ±0,05	2,8 ±0,05	2,65 ±0,03	3,13 ±0,04	6,51 ±0,08	10,95 ±0,13	13,99 ±0,16	25,75 ±0,36	71,16 ±1,13	31,45 ±0,40
	AB	2	135	3,1 ±0,08	2,6 ±0,08	2,59 ±0,04	3,37 ±0,06	6,46 ±0,12	10,33 ±0,14	13,47 ±0,17	25,60 ±0,51	71,06 ±1,32	30,94 ±0,36
	BB	2	73	3,6 ±0,09	2,8 ±0,14	2,61 ±0,06	3,03 ±0,06	6,50 ±0,14	11,46 ±0,29	14,95 ±0,30††	28,09 ±0,71	76,92 ±2,72	33,54 ±0,78
South	AA	6	248	3,1 ±0,07	2,6 ±0,06	—	3,70 ±0,07	—	—	—	27,53 ±0,37	71,68 ±1,47	—
	AB	4	185	3,4 ±0,08†	2,5 ±0,08	—	3,29 ±0,07	—	—	—	29,60 ±0,51	74,67 ±2,01	—
	BB	1	45	2,6 ±0,13	2,3 ±0,09	—	3,01 ±0,11	—	—	—	24,31 ±0,71	58,98 ±1,92	—

† significant at 5 % level.
†† significant at 1 % level.

For the significant differences, see the footnote to table 4.

among heterozygous. Lamb losses for AB rams were 2,2 %-units lower than for AA rams and 0,6 %-units lower than for BB rams. The percentage of lambs dying later was higher for AA and AB rams than for BB rams. The differences within regions were significant at the 0,05 level. Not surprisingly, the AA ♂ × AA ♀ mating type suffered greater losses than the other mating types.

3.2.1.4. Production characters

The problem in the present study is whether the biochemically defined populations show pronounced overlap in the distribution of production records. Since the variance in production characters is large, it is not surprising that the effects also have to be large before they are significant.

3.2.1.4.1. Ewe body weight and wool weight

Mean values in Tables 4, 5 and 7 show that ewes of haemoglobin type AA have a large and consistent superiority over AB and BB ewes. The differences attributed to haemoglobin types are rarely significant at accepted levels of probability. A comparison of body weight between the regions, showed that AA ewes in the north were, on average, 6,077 kg heavier ($P < 0,05$) than AB ewes and 3,554 kg heavier than BB ewes. A similar pattern was discovered in the eastern region, where AA ewes were 4,351 kg heavier in body weight than ewes of AB haemoglobin type. Wide variations in body weight were observed in the southern region, where AA ewes were 9,605 kg heavier ($P < 0,01$) than BB ewes and 1,712 kg heavier than AB ewes.

Results of wool weight, Tables 4, 5 and 7, show that ewes with AA haemoglobin type had small but consistent superiority over those ewes with AB and BB types. An extract from the analysis of variance shows that differences attributable to haemoglobin type are significant at the 0,05 level.

Table 9. Lamb mortality according to sex and ewe haemoglobin type.

Ewe Hb type	No. / %	Total											
		No. of lambs born		Born alive		Stillborn		0—3 days		4—14 days		14 days—4 months	
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
AA	No.	444	413	398	345	23	29	12	23	5	9	6	7
	%			89,6	83,5	5,2	7,0	2,7	5,6	1,1	2,2	1,4	1,7
AB	No.	292	305	259	276	9	9	11	11	7	5	6	4
	%			88,7	90,5	3,1	3,0	3,7	3,6	2,4	1,6	2,1	1,3
BB	No.	58	58	54	54	3	0	0	1	0	2	1	1
	%			93,1	93,1	5,2	0,0	0,0	1,7	0,0	3,5	1,7	1,7

Table 10. Lamb mortality according to ewe age and ewe haemoglobin type.

Ewe Hb type	Ewe age in year	No. of lambs born	Total									
			Born alive		Stillborn		0—3 days		4—14 days		14 days—4 months	
			No.	%	No.	%	No.	%	No.	%	No.	%
AA		121	94	77,7	15	12,4	7	5,8	3	2,5	2	1,7
AB	1 Yr.	130	110	84,6	8	6,2	6	4,6	5	3,8	1	0,8
BB		35	30	85,7	3	8,6	1	2,9	1	2,9	0	0,0
AA		244	215	88,1	15	6,1	10	4,1	2	0,8	2	0,8
AB	2 Yr.	180	160	88,9	9	5,0	6	3,3	2	1,1	3	1,7
BB		24	21	87,5	1	4,2	1	4,2	1	4,2	0	0,0
AA		518	434	83,8	47	9,1	19	3,7	9	1,7	9	1,7
AB	3 Yr.	319	265	83,1	28	10,6	15	4,7	5	1,6	6	1,8
BB		66	57	86,4	6	9,1	1	1,5	1	1,5	1	1,5

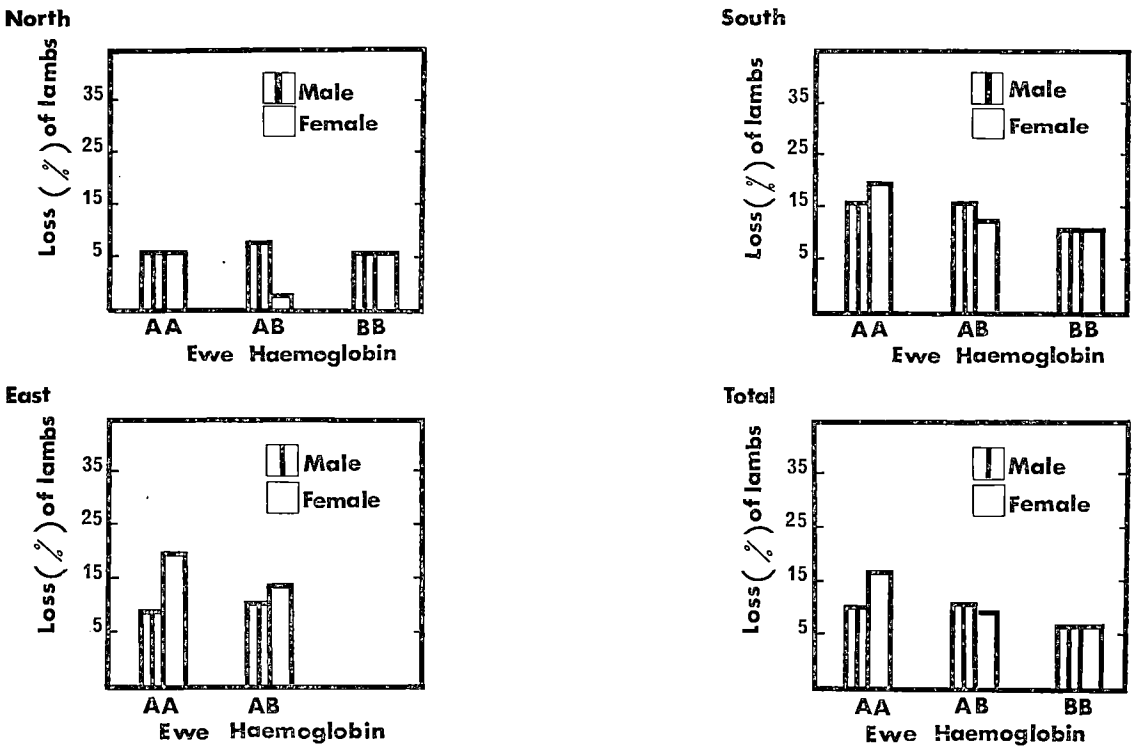


Fig. 7. Lamb mortality in different regions in relation to sex of lambs and ewe haemoglobin type.

In the northern region the fleece weight of AA ewes was greater than that of AB and BB ewes, 0,09 kg and 0,20 kg respectively. However, these differences were not significant. Surprisingly, AB ewes in the eastern region had wool weight which was 0,103 kg greater than that of AA ewes. The pattern in the southern region showed that ewes possessing AA haemoglobin type were the best ($P < 0,05$). AA ewes had a wool weight 0,509 kg and 0,703 kg greater than AB and BB ewes respectively.

3.2.1.4.2. Lamb weight at three days

The means of three-day lamb weights for different regions are given in Tables 5, 7 and 13 and correspondingly in Figure 8. Ewe haemoglobin type showed a relationship with the mean weight of lambs. In the northern region, ewes with AA haemoglobin type had 0,208 kg heavier lambs weighed at three days than those with AB type and 0,226 kg heavier lambs than BB ewes ($P < 0,05$). The mean lamb weight according to the age of ewe showed a similar pattern. The differences within the sire for the three-day lamb weights were consistently in favour of Hb AA ewes ($P < 0,05$). In the eastern region AA ewes had 0,111 kg heavier three-day-old lambs than AB ewes. Similarly in the southern region, AA ewes had 0,556 kg heavier three-day-old lambs than AB ewes.

The effect of ram haemoglobin type in Table 8 shows that there were only small differences between types as regards the mean weights. In the northern and eastern regions heterozygous rams had 0,022 kg heavier lambs at three days than had homozygous rams, and 0,338 kg heavier lambs than BB rams. However, these differences were not significant. The mating types AB rams to AA ewes and AA rams to AA ewes, had heavier three-day-old lambs than the other mating types (Table 5).

The mean weights of lambs of different phenotypes at three days are given in Tables 12 and 13. Small differences are noted between types. In the north, AA lambs were 0,070 kg and 0,132 kg heavier at three days than AB and BB lambs respectively. However, these differences were not significant. Similarly, in the eastern region, AA lambs were 0,052 kg heavier than AB type lambs. When one compares the mean weights of lambs with haemoglobin types in the south, one clearly sees that AA lambs showed more consistent superiority over AB and BB lambs (0,667 kg and 0,766 kg respectively). The difference was significant ($P < 0,05$).

3.2.1.4.3. Weaning weight of lambs

In Finland there is a great variation in the age of lambs at weaning and therefore a considerable variation occurs from region to region. The means of weaning weight of lambs are given in Tables 4, 5, 7 and 8. By comparing mean weights of lambs with haemoglobin types in the north, we can see that BB ewes were inferior to AA and AB ewes. The weaning weight of lambs was 1,777 kg smaller than for ewes of AA type and 0,993 kg smaller than for AB types. Results of weaning weight from the eastern region show again the superiority of AA ewes over AB and BB ewes. The differences in weaning weight were larger in the southern region, where BB ewes gave 4,032 kg and 2,437 kg smaller weaning weights from AA and AB types respectively. The differences were significant ($P < 0,01$).

Regarding the haemoglobin type of ram (Table 8), it can be noted that heterozygous rams were performing better than homozygous rams. Thus, not surprisingly, it was the AB ♂ × AA ♀ mating type which gave the highest weaning weight.

Considering lamb phenotypes (Tables 12 and 13) we see that in the north heterozygous lambs were 0,9 kg inferior in weaning weight to homozygous lambs. Lambs with BB haemoglobin in the eastern region had higher weaning weights than AA and AB lambs. However, these differences may be due to the small numbers of BB lambs. In the southern region there was a large difference between types, AA lambs having a higher weaning weight than AB or BB lambs. These differences were not significant.

Table 11. Lamb mortality according to ram haemoglobin type.

Sire Hb type	Total										
	No. of lambs born	Born alive		Stillborn		0—3 days		4—14 days		14 days—4 months	
	No.	No.	%	No.	%	No.	%	No.	%	No.	%
AA	803	672	83,6	73	9,1	31	3,9	12	1,5	15	1,9
AB	621	526	84,7	43	6,9	32	5,2	13	2,1	7	1,1
BB	214	188	87,8	16	7,5	4	1,9	3	1,4	3	1,4

Table 12. Performance of lambs of different sexes according to their haemoglobin type.

Lamb Hb type	Sex	No. of lambs	Birth weight kg	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
			$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
AA	Male	293	2,74±0,06	3,58±0,06	6,69±0,14	11,30±0,23	14,44±0,29	29,67±0,37	35,28±0,64
	Female ..	264	2,61±0,06	3,38±0,06	6,22±0,13	10,40±0,22	13,41±0,29	25,76±0,42	26,69±0,40
AB	Male	122	2,75±0,08	3,32±0,07	6,80±0,21	11,68±0,35	15,33±0,46	30,95±0,51	36,98±0,88
	Female ..	171	2,60±0,07	3,17±0,06	6,07±0,19	10,23±0,31	13,46±0,42	26,43±0,55	26,99±0,62
BB	Male	28	2,95±0,13	3,23±0,15	6,63±0,49	12,03±0,41	15,42±0,69†	31,39±0,69†	42,45±0,86†
	Female ..	40	2,60±0,17	3,16±0,10	6,48±0,50	12,59±0,74†	13,99±0,61	27,02±0,90	28,71±0,77

† significant at 5 % level.

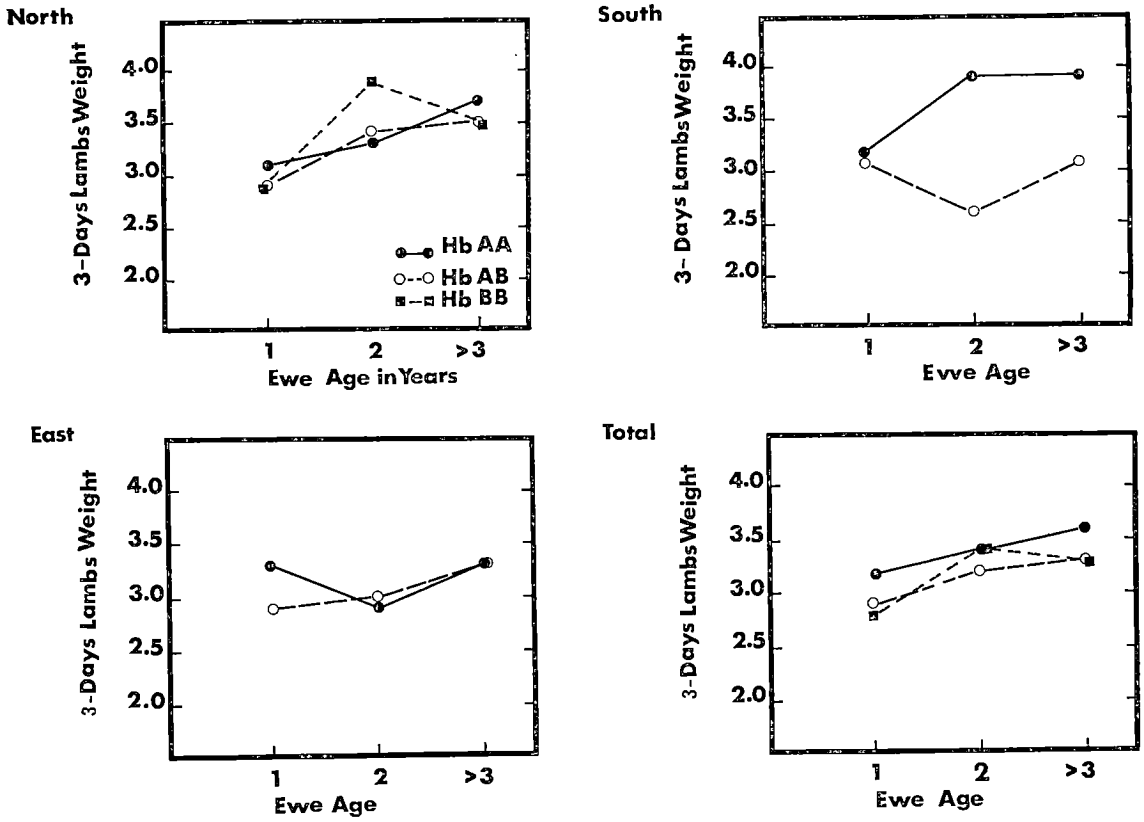


Fig. 8. The relationship between age of ewe and 3-day lamb weight according to ewe haemoglobin type in different regions.

Table 13. Performance of lambs according to haemoglobin type and region.

Region	Lamb Hb type	No. of lambs	Birth weight kg	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
			$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
North	AA	132	—	3,43±0,07	—	—	—	31,82±0,56	—
	AB	147	—	3,35±0,06	—	—	—	30,91±0,54	—
	BB	35	—	3,30±0,12	—	—	—	31,85±0,90	—
East	AA	223	2,69±0,04	3,15±0,07	6,50±0,10	10,93±0,17	14,01±0,21	26,10±0,45	31,78±0,50
	AB	96	2,68±0,05	3,10±0,07	6,42±0,14	10,94±0,25	14,36±0,33	26,25±0,65	31,88±0,75
	BB	24	2,75±0,12	3,30±0,16	6,54±0,34	12,35±0,84†	14,60±0,60	29,20±0,87	34,60±1,19†
South	AA	202	—	3,73±0,17†	—	—	—	27,92±0,43	—
	AB	50	—	3,07±0,12	—	—	—	25,81±0,90	—
	BB	19	—	2,97±0,15	—	—	—	24,53±0,99	—

† significant at 5 % level.

The results of the effect of ewe haemoglobin type on lamb litter weight are given in Table 4. According to MAIJALA and ÖSTERBERG (1976), litter weight is a product of litter size and growth rate and greatly determines the yield of lamb-meat per ewe. However, the superiority of AA ewes over both AB and BB ewes was seen again in all the three regions.

3.2.1.4.4. Weight of lambs at different ages

Data of lamb weight at birth, at three weeks, six weeks, eight weeks and five months of age were available from the two experimental flocks in the eastern region. The mean weights at the five different ages are presented, according to dam phenotype in Table 7, according to sire phenotype in Table 8, according to mating type in Table 5 and according to lamb phenotype in Tables 12 and 13.

The haemoglobin type of the dam had hardly any effect on the weights of the lambs. Only with one year old ewes was there a significant ($P < 0,05$) difference in weight of lambs at six weeks between ewes of Hb type AA and AB. Lambs born from AA ewe lambs were 0,813 kg heavier at six weeks than those born from AB ewe lambs.

With the haemoglobin type of sire too there was little difference between the weights of lambs at different ages, though the BB type tended to be superior to the other ones. Only in the six week and eight week weights were the differences statistically significant. Lambs from BB sire were 0,507 kg heavier at six weeks of age than those from AA sire ($P < 0,05$) and at eight weeks lambs from BB sire were 0,960 kg heavier than those from AA sire ($P < 0,01$). However, only one sire of BB type and one sire of AB type was represented in the study.

The mating type, e.g. the phenotype of sire and dam mated, had no significant effect on the lamb weights at either of the five ages. For weight at birth the mating type AB ram to AA ewe tended to be superior to the other mating types. However, the number of observations was very small. At six weeks and eight weeks the mating types AA ram to BB ewe and BB ram to AB ewe tended to be the best.

The phenotype of the lamb itself had a significant effect on the weight at six weeks and five months. In both cases the BB type was superior to the AA and AB types ($P < 0,01$ and $P < 0,05$, respectively).

3.2.2. Transferrins

3.2.2.1. Transferrin types

The transferrin types were observed and identified in order to their mobilities on the starch-gel. Five transferrin alleles were identified, Tf^A, Tf^B, Tf^C, Tf^D and Tf^E and 15 phenotypes produced by the diploid combinations of these alleles. As has been reported by ASHTON (1963), the product of the individual transferrin allele

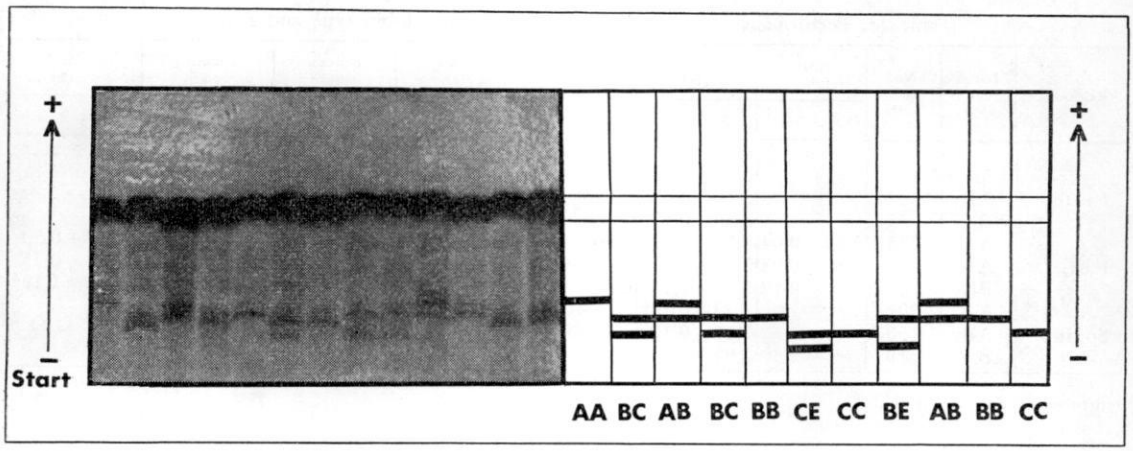


Fig. 9. A photograph of the transferrin described.
The schematic drawing gives the interpretation of the patterns presented by the transferrin types.

appears as two bands on the starch-gel, the one moving more slowly being the stronger. The A bands are the fastest and the E bands the slowest. They were comparable to the internationally known transferrin type standards, Tf^A, Tf^B, Tf^C, Tf^D and Tf^E obtained from Dr. Elizabeth Tucker, Cambridge, England. The electrophoretograms of various transferrin types are given in Figure 9.

3.2.2.2. Distribution of transferrin types

Distributions of transferrin phenotypes of Finnsheep in the three regions are given in Tables 14—16 and Fig. 10. Genotype and gene frequencies were estimated by the direct counting method from the relationships:

$$P = (2\,Tf\,AA + Tf\,AB + Tf\,AC + Tf\,AD + Tf\,AE)\,/2N$$
$$q = (2\,Tf\,BB + Tf\,AB + Tf\,BC + Tf\,BD + Tf\,BE)\,/2N$$
$$r = (2\,Tf\,CC + Tf\,AC + Tf\,BC + Tf\,CD + Tf\,CE)\,/2N$$
$$s = (2\,Tf\,DD + Tf\,AD + Tf\,BD + Tf\,CD + Tf\,DE)\,/2N \text{ and}$$
$$t = (2\,Tf\,EE + Tf\,AE + Tf\,BE + Tf\,CE + Tf\,DE)\,/2N,$$

where Tf AA, Tf AB, etc. are the numbers of animals of phenotype Tf AA, Tf AB, etc. found in any one group and N is the total number of animals in the group and where p, q, r, s and t represent the frequencies of the genes, Tf^A, Tf^B, Tf^C, Tf^D and Tf^E, respectively.

The frequencies of the transferrin alleles in the three regions of the present study are given in Table 14. Where an allele was absent, the frequency is given as 0. Frequencies of the five major alleles averaged: $Tf^A = 0{,}056$, $Tf^B = 0{,}226$, $Tf^C = 0{,}620$, $Tf^D = 0{,}075$ and $Tf^E = 0{,}023$. From the distribution of transferrin types it was revealed that the Tf^C was the commonest type in

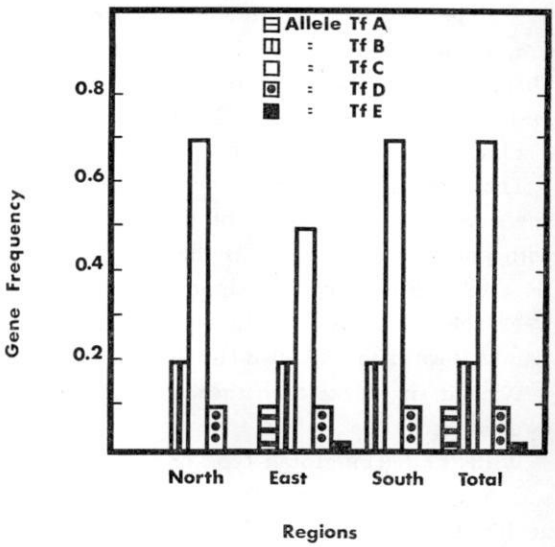


Fig. 10. The frequency of the alleles Tf^A, Tf^B, Tf^C, Tf^D, and Tf^E in different regions of the Finnsheep.

Table 14. Frequency distribution of transferrin phenotypes and the gene frequencies of transferrin A, B, C, D, and E in different regions.

Region	No. of animals	Transferrin phenotypes %														Gene frequency					Latitude	Meters above the sea level
		AA	AB	AC	AD	AE	BB	BC	BD	BE	CC	CD	CE	DD	DE	BE	Tf^A	Tf^B	Tf^C	Tf^D	Tf^E		
North	223	0,00	0,90	1,79	0,45	0,00	3,59	28,25	2,24	0,00	56,50	2,69	1,35	0,90	1,29	0,00	0,016	0,193	0,735	0,043	0,013	68°	150
East	425	1,18	2,82	10,35	3,77	0,94	4,94	31,06	4,94	2,59	25,65	6,59	4,00	0,94	0,00	0,24	0,101	0,257	0,516	0,086	0,040	62°	100
South	272	0,00	0,74	2,21	1,47	0,00	4,78	25,37	5,15	0,00	52,21	4,41	0,74	2,94	0,00	0,00	0,022	0,204	0,685	0,085	0,004	60°	45
Total	920	0,54	1,74	5,87	2,28	0,44	4,57	28,70	4,35	1,20	40,98	5,00	2,39	1,52	0,33	0,11	0,057	0,225	0,620	0,075	0,023		

Finnsheep ($P < 0,01$). In general, Tf^B and Tf^C were the commonest in each region and there was considerable variation in the frequencies of the transferrin alleles between animals born in different regions.

The ratios of phenotypes of the offspring of 312 matings, which agreed with the hypothesis that polymorphism is controlled by a series of five allelic genes Tf^A, Tf^B, Tf^C, Tf^D and Tf^E, are presented in Table 15. In the table, phenotypes designated Tf++ were all heterozygotes not possessing the gene examined in the particular mating. No offspring had a transferrin type incompatible with the assumption of a single locus model. Deviations from the expectations, calculated for each mating were, with one exception, not significant at the 5 % level of probability. This exception was for the matings between rams heterozygous for the Tf^C gene and ewes homozygous for it ($\chi^2 = 10,15$, 1 df, $P < 0,005$). A one to one ratio of homozygous to heterozygous offspring was expected from this mating, but in fact one out of fourteen offspring was heterozygous for the Tf^C gene.

Assuming random mating, the expected number of the 15 Tf phenotypes in all the three regions was calculated and compared with the observed number (Table 16). Deviations from the expected number were small and are due to chance. However, the χ^2 values did not reach the expected levels of significance, therefore the population may have attained Hardy-Weinberg equilibrium. There were excesses of CC phenotypes, whereas the number of CE phenotypes was smaller than the expected number. Therefore, the distribution of phenotypes containing Tf^C was tested separately. The deviations from expected numbers were too large to be caused by random sampling error only ($\chi^2 = 7,206$, 1 df, $0,01 > P > 0,001$), but because the material did not reflect a panmictic population, no conclusions can be drawn as to equilibrium conditions. The comparison of the eastern region and the northern and southern regions combined is of particular interest. The animals in the northern and southern regions were homogeneous with respect to gene frequency ($\chi^2 = 10,68$, 8 df,

Table 15. Distribution of transferrin phenotypes in the offspring of different matings in Finnsheep.

Mating type Ram × Ewe	No. of matings	Observed progeny ratios	x^2
		TfAA : TfA+ : Tf++	
TfAA × TfA+	6	6 : 8 : —	0,145
Tf++ × TfA+	78	— : 92 : 64	2,891
TfA+ × Tf++	9	— : 2 : 12	3,560
		TfBB : TfB+ : Tf++	
TfBB × TfB+	7	8 : 8 : —	0,000
TfB+ × TfB+	8	4 : 8 : 2	0,352
Tf++ × TfB+	55	— : 58 : 56	0,081
		TfCC : TfC+ : Tf++	
TfC+ × TfCC	12	26 : 2 : —	10,150†
TfC+ × TfC+	20	12 : 14 : 15	2,691
TfC+ × Tf++	54	— : 46 : 66	1,960
Tf++ × TfC+	12	— : 18 : 9	1 055
		TfDD : TfD+ : Tf++	
TfD+ × TfDD	10	12 : 15 : —	0,380
TfD+ × TfD+	18	16 : 24 : 12	0,880
		FfEE : TfE+ : Tf++	
TfE+ × Tf++	24	— : 38 : 18	3,441

† $P < 0,005$, df = 1.

$P = 0,1—0,05$), but pooled together, they were significantly different from the eastern animals ($\chi^2 = 13,69$, 5 df, $P = 0,02—0,01$).

3.2.2.3. Reproductive performance

The performance of ewes of different phenotypes in producing and rearing lambs is summarized in Table 17 and Fig. 11. The percentage of ewes of each phenotype, lambing in each region, showed considerable variation, but calculation showed that the trends in the number of lambs born were fairly clear in all phenotypes, although the effects were significant in AD phenotypes only. The most obvious feature was the superiority of AD ewes (+ 0,35 lambs) compared to the other phenotypes ($P < 0,05$).

Sextuplets occured among ewes of AC and BC phenotypes only. The highest percentage of lambs born as quintuplets were from parents of AD and CE phenotypes. AD ewes gave the highest proportion of quadruplets compared to other phenotypes ($P < 0,05$). The proportions of triplets, twins and singles were the highest for BD, CC and CE phenotypes respectively.

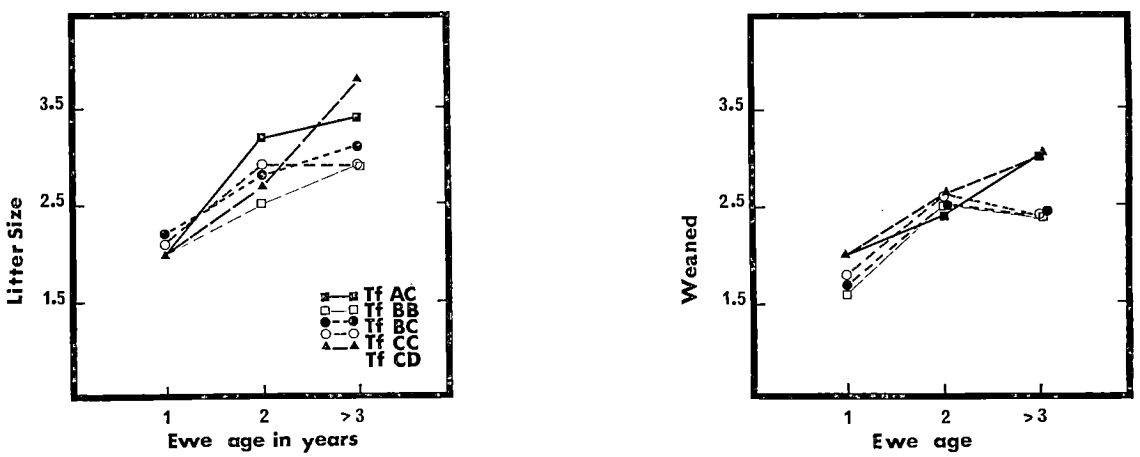


Fig. 11. The relationship between age of ewe and litter size and the number of lambs weaned of different transferrin types.

Table 16. Test of genetic equilibrium for transferrin types of Finnsheep in different regions.

Region		Transferrin phenotypes																df.	χ^2
		AA	AB	AC	AD	AE	BB	BC	BD	BE	CC	CD	CE	DD	DE	EE	Total		
North	obs.	0	2	4	1	0	8	63	5	0	126	6	3	2	3	0	223	4	3,508
	exp.	0,057	1,637	5,473	2,530	0,095	8,306	61,129	1,282	0,344	120,47	9,118	7,558	0,612	4,350	0,038	222,99		
East	obs.	5	12	44	16	4	21	132	21	11	109	28	17	4	0	1	425	4	2,301
	exp.	4,335	10,594	44,506	17,522	4,985	28,071	13,077	18,786	10,249	113,16	24,710	16,161	3,143	1,177	0,819	424,99		
South	obs.	0	2	6	4	0	15	67	14	0	145	15	2	8	0	0	272	4	3,851
	exp.	0,132	3,548	5,103	5,903	0,136	11,320	70,051	15,715	1,676	127,63	15,406	8,367	6,965	0,045	0,004	272,00		

Table 17. Means and standard errors of different production and reproduction measurements of ewes of different transferrin types.

Ewe Tf type	No. of ewes	Body weight	Wool weight	Litter size	Weaned	No. of lambs	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
		$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
AB	18	60,33±3,65	2,78±0,11	2,8±0,41	2,3±0,41	50	2,70±0,16	3,25±0,21	6,68±0,33	11,22±0,58	14,69±0,71	28,19±1,43	32,07±1,63
AC	17	55,50±2,47	2,62±0,14	3,1±0,31	2,7±0,28	53	2,75±0,14	3,41±0,16	6,30±0,26	10,01±0,42	12,69±0,50	25,76±1,04	28,84±1,07
AD	17	77,70±2,24	3,06±0,28	3,4±0,21†	3,1±0,26	58	2,54±0,12	3,63±0,15	6,66±0,17	10,97±0,35	14,40±0,48	26,03±1,50	32,38±1,80
BB	25	59,35±2,80	2,41±0,16	2,6±0,21	2,2±0,17	65	2,56±0,16	3,41±0,13	6,06±0,40	10,82±0,71	14,49±0,70	28,91±0,77	34,69±2,06
BC	129	56,98±1,10	2,33±0,08	2,8±0,09	2,3±0,08	360	2,62±0,06	3,31±0,05	7,54±0,15††	11,26±0,23	14,36±0,23	29,02±0,38	33,18±0,73
BD	28	63,16±1,94	2,50±0,10	2,9±0,22	2,3±0,44	82	2,67±0,06	3,38±0,10	6,78±0,13	11,17±0,23	14,55±0,29	27,97±0,60	31,50±0,74
CC	210	53,81±0,98	2,22±0,06	2,7±0,07	2,3±0,06	562	2,68±0,06	3,00±0,04	7,69±0,16††	11,38±0,26	14,44±0,34	28,75±0,32	32,05±0,80
CD	24	55,09±2,12	2,64±0,13	2,9±0,23	2,6±0,21	70	2,63±0,09	3,22±0,11	6,56±0,19	11,36±0,45	14,12±0,52	27,13±0,88	31,91±1,19
CE	7	54,08±5,93	2,17±0,31	2,9±0,43	2,6±0,53	20	2,69±0,13	3,25±0,22	6,19±0,40	10,89±0,64	13,95±0,69	23,56±1,39	28,03±1,46
DD	17	65,59±2,68	2,51±0,15	3,3±0,25	2,4±0,28	56	2,58±0,07	3,42±0,13	5,71±0,22	9,01±0,38	12,67±0,48	25,70±0,97	27,91±0,83

† significant at 5 % level.
†† significant at 1 % level.

For the signifigant differences, see the footnote to table 4.

As regards the performance of the ram (Table 18), it can be seen that in the northern region CC rams gave + 0,5 more lambs than did other phenotypes. Similarly, in the South, CC rams appeared to have the largest litters, the differences being significant at the 0,05 level, whereas in the eastern region, the number of lambs born was the highest (P < 0,05) for the BB rams and the average litter size was 3,40 lambs.

The number of lambs at weaning (Table 19) showed large variation from region to region. This proportion was affected by the different ages of the ewes in this sample and also by climatic conditions. However, the results for the different transferrin types suggest that CD ewes were superior to other phenotypes in respect to the number of lambs weaned. As regards the phenotypes of the rams (Table 18), BB rams had the best performance as to the number of lambs weaned (P < 0,05).

The BC ♂ × AC ♀ mating type gave the highest number for both lambs born (4,0), and lambs weaned, (3,6) (P < 0,05).

3.2.2.3.1. Lamb mortality

Mortality in lambs from birth to 3 days, 4—14 days and from 14 days to 4 months, in the three regions is given in Tables 20 and 21 and is further illustrated in Fig. 12. The proportion of dead male and female lambs within each age group is included.

The percentage of lambs dead for ewes of different transferrin phenotype and of different ages varied from region to region (Table 20), but it appeared that the losses for BD ewes were higher than for ewes of other phenotypes (20,7 % vs 14,7 %). The differences between phenotypes within farms were significant (P < 0,01). The range of stillbirths for different phenotypes varied from 1,8 % in DD ewes to 10,5 % in BC ewes. From birth to 3 days, losses were heavy (P < 0,05) in AD and BD ewes (6,8 %), whereas losses were lighter in CC ewes (2.8 %). Considering mortality from 4—14 days and from 14 days up to 4 months

Table 18. Means and standard errors of reproduction and production characters of rams of different transferrin types according to region.

Region	Ram Tf type	No. of ewes mated	Litter size	Weaned	No. of lambs	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
			x̄ ± SE	x̄ ± SE		x̄ ± SE	x̄ ± SE	x̄ ± SE	x̄ ± SE	x̄ ± SE	x̄ ± SE	x̄ ± SE
North	AB	30	2,2±0,10	2,1±0,10	67	—	3,08±0,06	—	—	—	29,65±0,73	—
	BC	63	2,6±0,13	2,4±0,13	166	—	3,35±0,03	—	—	—	30,52±0,22	—
	CC	68	2,7±0,12	2,4±0,10	181	—	3,38±0,06	—	—	—	32,07±0,36†	—
East	AB	40	3,0±0,17	2,4±0,14	119	2,72±0,06	3,26±0,08	6,48±0,14	10,94±0,24	14,01±0,29	26,08±0,61	32,12±0,68
	AC	14	3,1±0,32	2,4±0,29	43	2,54±0,09	3,05±0,12	6,53±0,26	10,79±0,41	13,85±0,47	25,78±0,96	31,64±1,20
	BB	14	3,4±0,27†	3,1±0,27†	47	2,71±0,08	3,01±0,09	6,30±0,24	11,02±0,38	13,91±0,48	25,53±1,04	30,91±1,12
	BC	16	2,3±0,28	2,7±0,31	52	2,74±0,08	3,28±0,09	6,87±0,15	11,52±0,29	14,87±0,38	26,34±0,97	31,77±0,99
	CC	38	3,1±0,13	2,6±0,16	119	2,57±0,05	2,97±0,05	6,48±0,11	11,09±0,21	14,30±0,24	26,61±0,56	32,23±0,64
	CE	12	3,1±0,36	2,5±0,34	37	2,56±0,09	3,08±0,11	6,51±0,25	10,87±0,44	13,80±0,56	26,00±1,16	31,11±1,24
South	BC	21	2,6±0,24	2,0±0,20	54	—	3,54±0,11	—	—	—	30,29±0,96††	—
	CC	110	2,9±0,12†	2,4±0,09	319	—	3,65±0,06	—	—	—	28,17±0,35	—
	CE	17	2,2±0,19	1,9±0,18	37	—	3,04±0,13	—	—	—	25,36±0,81	—

† significant at 5 % level.
†† significant at 1 % level.

Table 19. Means and standard errors of reproduction and production characters of ewes of different transferrin types in different regions.

Region	Ewe Tf type	No. of ewes	Body weight	Wool weight	Litter size	Weaned	No. of lambs	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
			$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
North	AC	4	53,00±1,89	1,95±0,04	3,5±1,03	3,2±0,87	15	—	3,39±0,16†	—	—	—	26,29±1,22	—
	BB	8	51,00±5,85	1,56±0,08	2,3±0,25	2,1±0,23	18	—	3,11±0,16	—	—	—	32,71±0,78	—
	BC	43	53,74±4,82	1,85±0,25	2,7±0,42	2,2±0,31	118	—	3,30±0,06	—	—	—	32,98±0,45††	—
	BD	5	67,00±1,83	2,23±0,11	2,8±0,58	2,8±0,58	14	—	3,37±0,21	—	—	—	33,18±1,10††	—
	CC	93	51,86±6,34	1,97±0,38	2,5±0,38	2,3±0,39	235	—	3,29±0,04	—	—	—	30,89±0,37	—
	CD	8	55,40±6,09	2,02±0,12	2,0±0,26	2,0±0,26†	16	—	3,52±0,25	—	—	—	28,73±1,39	—
	CE	3	52,00±2,45	1,15±0,04	1,7±0,67	1,7±0,67	5	—	3,88±0,71	—	—	—	26,25±2,44	—
	DD	5	70,00±3,75	2,10±0,06	2,8±0,20	2,6±0,25	14	—	3,27±0,18	—	—	—	28,33±0,87	—
East	AB	5	58,60±5,28	2,70±0,08	3,2±0,49	2,6±0,40	16	2,70±0,18	3,57±0,20	6,68±0,68	11,27±0,68	14,69±0,83	27,89±1,92	32,07±1,92
	AC	7	52,07±2,89	2,94±0,15	3,0±0,44	2,7±0,36	21	2,75±0,12	3,07±0,16	6,30±0,25	10,01±0,40	12,69±0,48	23,67±0,94	28,84±1,01
	BB	4	56,33±5,95	3,03±0,25	3,8±0,25	2,5±0,65	15	2,56±0,14	2,90±0,14	6,06±0,32	10,82±0,58	14,49±0,58	28,41±1,56	34,69±1,68
	BC	38	54,76±1,96	2,60±0,14	3,1±0,13	2,5±0,16	116	2,62±0,06	3,13±0,06	6,54±0,13	11,16±0,21	14,36±0,25	27,45±0,58	33,18±0,66
	BD	9	59,17±3,15	2,61±0,13	3,1±0,39	2,7±0,29	28	2,67±0,10	3,16±0,12	6,78±0,23	11,37±0,40	14,55±0,49	26,38±0,49	31,50±1,26
	CC	43	51,49±1,68	2,50±0,07	2,9±0,14	2,2±0,14	123	2,68±0,05	3,11±0,08	6,68±0,14	11,18±0,23	14,42±0,30	26,24±0,63	32,05±0,71
	CD	16	54,99±3,01	2,84±0,19	3,2±0,26	2,7±0,24†	51	2,63±0,08	3,14±0,10	6,56±0,17	11,36±0,41	14,12±0,47	26,32±1,02	31,91±1,06
	CE	4	55,13±5,01	2,68±0,13	3,8±0,75	3,3±0,75	15	2,69±0,15	3,03±0,15	6,19±0,46	10,89±0,74	13,95±0,80	22,73±1,42	28,03±1,69
	DD	4	61,88±3,76	2,43±0,21	4,8±0,25	4,5±0,29	19	2,58±0,11	3,01±0,17	5,71±0,37	9,91±0,64	12,67±0,82	21,88±1,29	27,91±1,43
South	AC	6	72,33±3,06	2,88±0,28	2,8±0,31	2,0±0,26	17	—	3,78±0,27	—	—	—	28,58±2,08†	—
	AD	4	77,75±2,84	2,95±0,47	4,0±0,41	3,5±0,29	16	—	3,84±0,22†	—	—	—	26,19±2,02	—
	BB	13	63,54±2,80	2,89±0,14	2,5±0,31	2,2±0,25	32	—	3,72±0,19	—	—	—	26,52±0,95	—
	BC	48	66,02±1,63	2,67±0,12	2,6±0,14	2,2±0,13	126	—	3,45±0,09	—	—	—	28,15±0,48††	—
	BD	14	67,07±2,80	3,09±0,33	2,9±0,33	1,9±0,27	40	—	3,54±0,17	—	—	—	27,28±0,69	—
	CC	74	68,08±1,13	2,81±0,10	2,8±0,13	2,3±0,10	204	—	3,07±0,17	—	—	—	27,95±0,47	—
	DD	8	65,75±3,83	2,73±0,19	2,9±0,35	2,4±0,32	23	—	3,71±0,25	—	—	—	27,50±1,69	—

† significant at 5 % level.
†† significant at 1 % level.

For the significant differences, see footnote to table 4.

Table 20. Lamb mortality of ewes of different transferrin types.

Ewe Tf type	No. / %	Total												Total					
		Total lamb born		Born alive		Still-born		0—3 days		4—14 days		14days—4 months		Total lamb born	Born alive	Still-born	0—3 days	4—14 days	14days—4 months
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀						
AB	No.	8	13	8	10	0	1	0	1	0	0	0	1	22	18	2	1	0	1
	%			100	76,9	0,0	7,7	0,0	7,7	0,0	0,0	0,0	7,7		81,8	9,1	4,5	0,0	4,5
AC	No.	19	33	17	28	2	1	0	2	0	1	0	1	53	45	4	2	1	1
	%			89,5	84,9	10,5	3,0	0,0	6,1	0,0	3,0	0,0	3,0		84,9	7,5	3,8	1,9	1,9
AD	No.	14	13	10	12	1	0	1	1	1	0	1	0	27	22	1	2	1	1
	%			71,4	92,3	7,1	0,0	7,1	7,1	7,1	0,0	7,1	0,0		81,5	3,7	7,4	3,7	3,7
BB	No.	30	31	27	28	1	1	1	1	0	1	1	0	65	55	6	2	1	1
	%			90,0	90,3	3,3	3,2	3,3	3,2	0,0	3,2	3,3	0,0		84,6	9,2	3,1	1,5	1,5
BC	No.	171	167	155	140	7	14	4	7	4	3	1	3	360	295	39	15	7	4
	%			90,6	83,8	4,1	8,4	2,3	4,2	2,3	1,8	0,6	1,8		81,9	10,8	4,2	1,9	1,1
BD	No.	42	39	38	27	2	4	1	4	0	3	1	1	82	65	7	5	3	2
	%			90,5	69,2	4,8	10,3	2,4	10,2	0,0	7,7	2,4	2,6		79,3	8,5	6,1	3,7	2,4
CC	No.	303	242	264	216	18	13	9	7	6	4	6	2	562	480	48	16	10	8
	%			87,1	89,2	5,9	5,4	3,0	2,9	2,0	1,7	2,0	0,8		85,4	8,5	2,8	1,8	1,4
CD	No.	35	34	31	31	2	2	0	0	0	0	2	1	70	62	5	0	0	3
	%			88,6	91,2	5,7	5,9	0,0	0,0	0,0	0,0	5,7	2,9		88,6	7,1	0,0	0,0	4,3
CE	No.	7	13	6	12	1	0	0	0	0	1	0	0	20	18	1	0	1	0
	%			85,7	92,3	14,3	0,0	0,0	0,0	0,0	7,7	0,0	0,0		90,0	5,0	0,0	5,0	0,0
DD	No.	26	29	24	26	1	0	0	2	0	0	1	1	56	50	1	3	0	2
	%			92,3	89,7	3,9	0,0	0,0	6,9	0,0	0,0	3,9	3,4		89,3	1,8	5,4	0,0	3,6

AD ewes suffered greater losses in comparison to CC ewes (3,7 % vs 1,6 %). However, the differences were not significant.

The lamb mortality varied according to the phenotype of the ewe and according to her age. In BC ewes there was a rapid decline from 20,7 % in ewe lambs to 12,4 % in two-year-old ewes ($P < 0,01$), then there was a slight increase again in the there-year-old ewes. A similar pattern was obtained in CC ewes. On the other hand, the percentages of lambs dead in BD ewes decreased with increasing age of the ewe. The age of the ewe did not seem to have any effect on lamb mortality.

Table 20 gives losses of lambs for ewes of each transferrin type according to the sex of the lambs. The mortality of male lambs was the highest for ewes of AD phenotype (28,6 %), whereas that of female lambs was the highest in BD ewes (30,8 %). These differences, however,

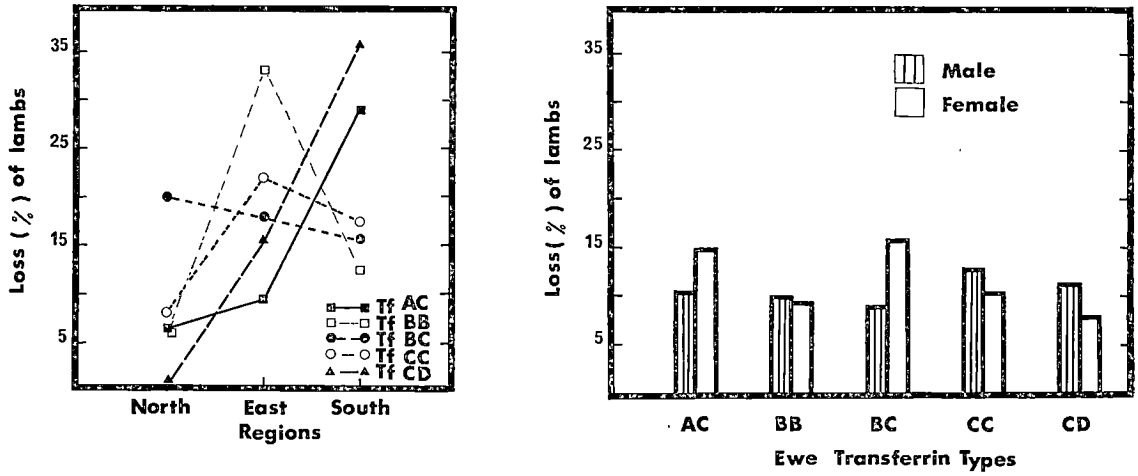


Fig. 12. Lamb mortality in relation to different regions and lamb sex of different ewe transferrin types.

Table 21. Lamb mortality of rams of different transferrin types.

Ram Tf type	No. / %	Total										Total					
		Total lamb born		Born alive		Still-born		0—3 days		4—14 days		14days—4 months		Total lamb born	Born alive	Still-born	0—3 days	4—14 days	14days—4 months
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀						
AB	No.	102	77	96	63	2	5	0	4	1	3	3	2	186	159	14	4	4	5
	%			94,1	81,8	2,0	6,5	0,0	5,4	1,0	3,9	2,9	2,6		85,5	7,5	2,2	2,2	2,7
AC	No.	24	18	18	16	4	0	0	1	1	0	1	1	43	34	5	1	1	2
	%			75,0	88,8	16,7	0,0	0,0	5,6	4,1	0,0	4,1	5,6		79,1	11,6	2,3	2,3	4,7
BB	No.	24	23	22	21	1	1	1	1	0	0	0	0	47	43	2	2	0	0
	%			91,7	91,3	4,1	4,3	4,1	4,3	0,0	0,0	0,0	0,0		91,5	4,3	4,3	0,0	0,0
BC	No.	136	125	123	111	8	6	3	5	0	2	2	1	272	234	25	8	2	3
	%			90,4	88,8	5,9	4,8	2,2	4,0	0,0	1,6	1,5	0,8		86,0	9,2	2,9	0,7	1,1
CC	No.	301	305	257	264	18	17	11	13	9	8	6	3	619	521	47	25	17	9
	%			85,3	86,6	6,0	5,6	3,7	4,2	3,0	2,6	2,0	1,0		84,2	7,6	4,0	2,7	1,5
CE	No.	36	36	34	29	0	4	1	0	0	0	1	3	74	63	6	1	0	4
	%			94,4	80,6	0,0	11,1	2,8	0,0	0,0	0,0	2,8	8,3		85,1	8,1	1,4	0,0	5,4

were not significant. The percentage of losses in male and female lambs was similar for the BB phenotype. No explanation can be given for the abnormal sex ratio at birth.

Considering sire transferrin type and its relationship to lamb mortality, Table 21 shows that rams of AC phenotype suffered greater losses than the other phenotypes (20,9 % vs 14,8 %). The lamb losses were remarkably smaller (8,5 %) for BB phenotype. These differences, however, were not significant. The proportion of stillborn lambs was much higher among rams of AC phenotypes than among those of BB phenotypes (11,6 % vs 4,3 %). The percentage of lambs that died between birth and 3 days was the highest in BB rams (4,3 %); the lowest percentage was observed in CE rams (1,4 %), and this difference was significant ($P < 0,05$). Certainly lamb mortality in general is also affected by factors like number of lambs born and small weak lambs at birth and poor growth rate as well as inappropriate nutrition during gestation.

Mortality from birth to weaning was the highest ($P < 0,01$) among the offspring of BC ♂ × BD ♀ mating type and the average litter size at birth and weaning was 3,5 and 1,5 lambs respectively.

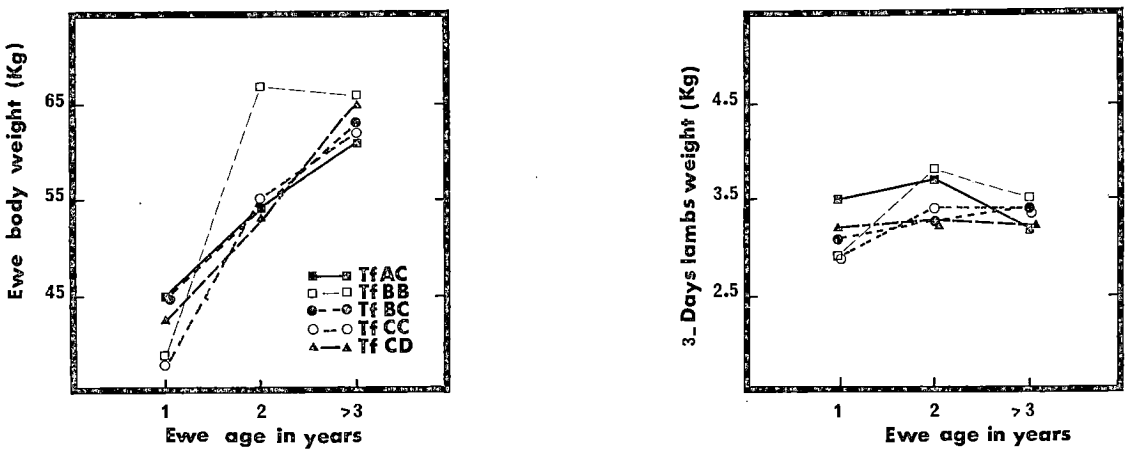


Fig. 13. The relationship between age of ewe and ewe body weight and 3-day lamb weight with respect to ewe transferrin types.

3.2.2.4. Production characters

3.2.2.4.1. Ewe body weight and wool weight

Tables 17 and 19 and Figure 13 give the means and standard errors of ewe body weight and wool weight for ewes of different transferrin phenotypes. There was a large variation between and within each region. This variation was also partly due to the age-differences of the ewes, the variation in environmental conditions and in the numbers of the observations. AD ewes showed a larger and more consistent superiority over the other phenotypes. The differences were not significant at an accepted level of probability. However, a comparison of body weight within regions showed that northern DD ewes were 10,1 kg heavier ($P < 0,05$) than ewes of other phenotypes. In the eastern region, DD ewes were 6,57 kg heavier ($P < 0,05$) than the other types. AD ewes had heavier body weight in the southern region, weighing 10,7 kg more than the other phenotypes ($P < 0,05$).

The effect of transferrin types on fleece weight is given in Tables 17 and 19. The trend shows that ewes of AD transferrin type had the heaviest wool weights and showed a consistent superiority over the other phenotypes (3,1 kg vs 2,5 kg per year), although the effect just failed to reach significance at an accepted level of probability. As regards wool weights, in the north, BD ewes produced the greatest. Similarly, in the southern region, BD ewes yielded the greatest weight of wool (3,09 kg vs 2,83 kg per year). The pattern in the East shows that BB ewes gave greater wool weights than the other phenotypes (3,03 kg vs 2,56 kg per year). Again, however, the results did not show significant heterogeneity, neither within nor between the regions.

3.2.2.4.2. Lamb weight at three days

The means and standard errors of the 3-day lamb weights for each transferrin phenotype of the ewe in the three regions are given in Tables 17 and 19 and Fig. 13. The differences in lamb weights at 3-days of age of ewes of different transferrin types show that there is considerable variation between regions. In the northern region, heterozygous ewes gave heavier lambs than homozygous ewes (3,5 vs 3,0 kg). The differences were significant for AC ewes at the 0,05 level. In eastern Finland, AB ewes were superior to the other phenotypes (3,6 vs 3,1 kg). However, these differences were not significant at an accepted level of probability. Results of the three-day lamb weight from southern Finland show that lambs born from from CC ewes were inferior in weight to those born from AC, AD, BB and DD ewes (3,4 vs 3,8 kg).

Regarding ram transferrin type and its relationship to 3-day lamb weight (Table 18), lambs sired by CC phenotypes in the northern and southern regions were heavier than lambs sired by AB, BC and CE phenotypes. The differences were not significant. The superiority of BC rams was seen in the eastern region, but the differences were not significant.

Table 22. Means and standard errors of weights (kg) of lambs of different transferrin types.

Lamb Tf type	No. of lambs	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
		$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
AB	10	2,46±0,26	3,10±0,23	5,95±0,48	9,69±0,32	13,13±0,89	23,42±1,66	27,48±1,54
AC	36	2,76±0,10	3,17±0,14	6,57±0,26	10,93±0,41	14,10±0,43	27,89±0,93	34,23±1,06
AD	18	2,81±0,14	3,43±0,19	6,57±0,35	11,19±0,81	14,66±1,08	27,48±1,96	32,14±1,13
BB	16	2,48±0,08	2,86±0,13	6,49±0,33	11,30±0,43	15,07±0,49	26,82±1,38	33,21±1,45
BC	128	2,77±0,05	3,36±0,08	6,46±0,13	11,06±0,21	14,20±0,25	27,86±0,54	32,61±0,65
BD	23	2,74±0,14	3,19±0,17	6,82±0,37	11,00±0,39	14,03±0,75	24,90±1,33	30,43±1,63
CC	157	2,63±0,04	3,44±0,07	6,59±0,11	11,23±0,21	14,40±0,22	28,28±0,53	32,63±0,57
CD	22	2,77±0,12	3,65±0,25	6,38±0,13	10,28±0,21	13,20±0,31	26,74±1,67	27,12±0,92
CE	12	2,62±0,12	3,33±0,13	6,19±0,40	10,03±0,58	12,63±0,73	23,96±1,29	29,31±1,92

Table 23. Means and standard errors of lamb weights (kg) of different lamb transferrin types according to the sex.

Lamb Tf type	Lamb sex	No. of lambs	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
			$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
AC	Male	22	2,73±0,14	3,33±0,83	6,61±0,35	10,82±0,54	13,76±0,59	29,10±1,24	36,72±1,37
	Female ..	14	2,81±0,16	2,80±0,18	6,49±0,38	11,10±0,69	14,54±0,71	26,00±1,27	30,31±1,01
AD	Male	8	3,10±0,23	3,78±0,51	7,20±0,55	13,28±1,25	16,58±1,63	33,46±2,43	39,79±2,36
	Female ..	10	2,58±0,13	3,08±0,16	6,07±0,40	09,52±0,78	13,13±1,34	22,70±1,91	26,02±1,53
BB	Male	11	2,48±0,09	2,98±0,19	6,48±0,51	11,46±0,65	15,06±0,64	28,71±1,53	35,91±1,56
	Female ..	5	2,48±0,21	2,57±0,24	6,52±0,26	10,98±0,39	15,13±0,78	22,66±1,96	27,80±1,73
BC	Male	69	2,83±0,09	3,46±0,13	6,71±0,21	11,53±0,35	14,97±0,44	30,43±0,65	37,05±0,87
	Female ..	59	2,68±0,07	3,23±0,12	6,14±0,19	10,44±0,31	13,27±0,37	24,80±0,75	26,72±0,56
BD	Male	12	3,03±0,19	3,67±0,26	7,03±0,51	11,95±0,84	15,26±1,06	29,03±1,76	35,17±2,16
	Female ..	11	2,43±0,17	2,82±0,26	5,70±0,51	9,96±0,76	12,69±0,94	20,41±1,02	25,26±1,22
CC	Male	81	2,64±0,08	3,55±0,13	6,72±0,23	11,33±0,37	14,81±0,46	30,76±0,68	35,90±1,25
	Female ..	76	2,61±0,08	3,33±0,10	6,40±0,24	11,09±0,58	13,80±0,53	25,32±0,71	27,87±0,74
CD	Male	9	3,00±0,24	3,52±0,31	7,00±0,40	10,10±0,16	11,70±0,55	30,73±2,72	30,60±1,45
	Female ..	13	2,67±0,20	3,43±0,25	6,18±0,15	10,33±0,34	13,70±0,62	23,97±1,38	25,96±1,07

Results for lambs of different phenotypes are summarized in Tables 22 and 23. The three-day weight of lambs of each phenotype in each region shows a slight but not significant variation. This variation may be due to sampling error. However, heterozygous lambs were heavier than homozyous lambs, and it seems that the C allele had some effect on lamb weight.

sired by other phenotypes. In the southern region the performance of BC rams was the best compared to other phenotypes and the differences within region were significant ($P < 0,01$).

Tables 22 and 23 show that heterozygous lambs were superior in weight to homozygous ones and that the C allele seemed to have an effect on lamb weights.

3.2.2.4.3. Weaning weights of lambs

The weaning weights of lambs according to ewe transferrin type are presented in Tables 17 and 19. Comparison of weaning weights of lambs from ewes of different transferrin types indicates substantial differences between types and regions. It should further be noted that weaning weight was also affected by breeding system, litter size, lamb mortality and feeding systems. In the northern region lambs from BC and BD ewes were 4 kg heavier than those from other phenotypes ($P < 0,01$). Similarly, in the southern region, lambs born from AC and BC ewes were 1,4 kg heavier than those born from other phenotypes, but this was not significant. As regards ram phenotypes, Table 18, we note that in the northern region, lambs sired by CC phenotypes were 2,0 kg heavier than those sired by other phenotypes ($P < 0,05$). In the eastern region, lambs sired by AC and BB rams were almost 1,0 kg lighter than those

3.2.2.4.4. Weights of lambs at different ages

The mean weights of lambs at birth, three weeks, six weeks, eight weeks and five months which were available from the experimental flock in the eastern region, are given according to the transferrin type of the dam in Tables 17 and 19, according to the transferrin type of the sire in Table 18 and according to the transferrin type of the lamb itself in Tables 22 and 23.

The Tf type of the dam had no significant effect on the birth weight of the lambs, but at three weeks ewes of BC and CC types have a significant ($P < 0,01$) effect on the lamb weights. As regards six and eight week weights of lambs, dams of DD type were significantly ($P < 0,01$) inferior to dams of BC and CC types. As regards five month weights there was a considerable difference between dams of BB and DD types, BB type being the better and DD the worse, but the difference was not significant.

The Tf type of the sire had no significant effect on the weights of lambs at any of the five ages, although sires of BC type had the heaviest offspring at six and eight weeks of age.

The difference between phenotypes of lambs were not significant at any of the five ages, but at six and eight weeks, the BB lambs were the heaviest, and at eight weeks, the CE lambs were the lightest.

3.2.3. Potassium

3.2.3.1. Potassium types

The whole blood potassium concentration was determined by using an Atomic Absorption Spectrophotometer. The plasma K^+ content is negligible when compared to the erythrocyte K^+ content. Therefore, results obtained from analysis of whole blood represent erythrocyte contents.

The sheep were classified into two distinct types according to the potassium concentrations in their blood (EVANS, 1954). The reading was expressed in mEq/litre RBC. The individuals with whole blood potassium concentration below or equal to 70 mEq/litre were classified as low-potassium (LK), whereas those having more than 70 mEq/litre were classified as high-potassium (HK). The two distributions revealed a marked kurtosis. Leptokurtosis exists at the low potassium level and platokurtosis at the high potassium level.

3.2.3.2. Distribution of potassium types

Table 24 and Fig. 14 show the frequencies of the different phenotypes for red blood cell potassium in 760 animals in which complete data were obtained. 80 % of Finnsheep were of high potassium type (HK) and 20 % of low potassium type (LK). The highest percentage of HK animals was found in southern Finland. There was a slight, but not significant difference in the distribution of potassium types between southern Finland and the eastern region. However, high potassium type (HK) predominated in Finnesheep.

Genetic control of potassium types in Finnsheep was also studied. Table 25 summarizes the data on the inheritance of the HK and LK types for the sheep. All lambs were tested when they were at least 3 months old. Observations of inheritance of potassium types furnished further evidence to support the concept that potassium types in sheep are genetically determined by a simple allelic pair the K^L type being dominant over the K^H type and inherited in a simple Mendelian manner. The HK animals

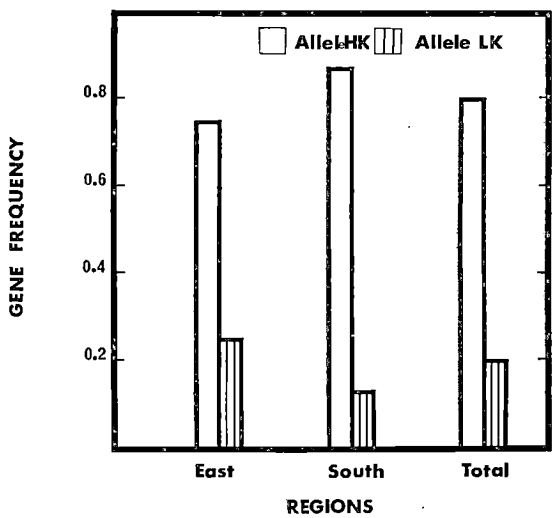


Fig. 14. The frequency of the high-potassium (K^H) and low-potassium (K^L) alleles in different regions of Finnsheep.

Table 24. Frequency distribution of potassium phenotypes and the gene frequency of high and low potassium in different regions.

Region	No. of animal	Potassium phenotype %		Gene frequency		Latitude	Meters above the sea level
		HK	LK	K^H	K^L		
East	453	75,50	24,50	0,76	0,25	62°	100
South	307	86,97	13,03	0,87	0,13	60°	45
Total	760	80,13	19,87	0,80	0,20		

Table 25. Distribution of potassium phenotypes in the offspring from four different matings.

Phenotype of parents	No. of sires	No. of dams	Eastern region			No. of sires	No. of dams	Southern region			No. of sires	No. of dams	Total		
			Distribution of phenotypes					Distribution of phenotypes					Distribution of phenotypes		
Sirexdam			HK	LK	Total			HK	LK	Total			HK	LK	Total
HK × HK ..	3	69	136	—	136	7	153	105	—	105	10	222	241	—	241
HK × LK ..	2	13	10	14	24	6	22	13	7	20	8	35	23	21	44
LK × HK ..	4	51	61	44	105	—	—	—	—	—	4	51	61	44	105
LK × LK ..	4	12	6	16	22	—	—	—	—	—	4	12	6	16	22
Total	13	145	213	74	287	13	175	118	7	125	26	320	331	81	412

Table 26. Test of genetic equilibrium in lambs of Finnsheep.

Phenotype of parents Sire × dam	No. of matings	Phenotypes of offspring				$x^2(_1)$
		High potassium		Low potassium		
		observed	expected	observed	expected	
HK × HK	24	24	24	—	—	0,000
HK × LK	12	7	5,52	5	6,48	0,733
LK × HK	9	3	4,14	6	4,86	0,581
LK × LK	4	2	0,84	2	3,16	2,393
Total of last 3 classes	25	12	10,50	13	14,50	0,369

can therefore be regarded as homozygous for one allele, whereas the LK animals are either heterozygous or homozygous for the other allele.

Testing for genetic equilibrium in 49 matings in the eastern region shows a shortage of 6,0 per cent in HK offspring (Table 26). This shortage in the whole population was small, and it was very unevenly spread over the various matings. The order of the mating of these types in the population was random, as is evident from an insignificant χ^2 of 0,369 as a result of segregating matings. The insignificant chi-square for heterogeneity shows that sampling errors cannot be excluded as the cause of this shortage in HK.

3.2.3.3. Reproductive performance

The numbers of lambs born and weaned from both known parents and for the two regions (southern and eastern Finland) are given in Tables 27—30 and further illustrated in Figure 15. There were differences between the two

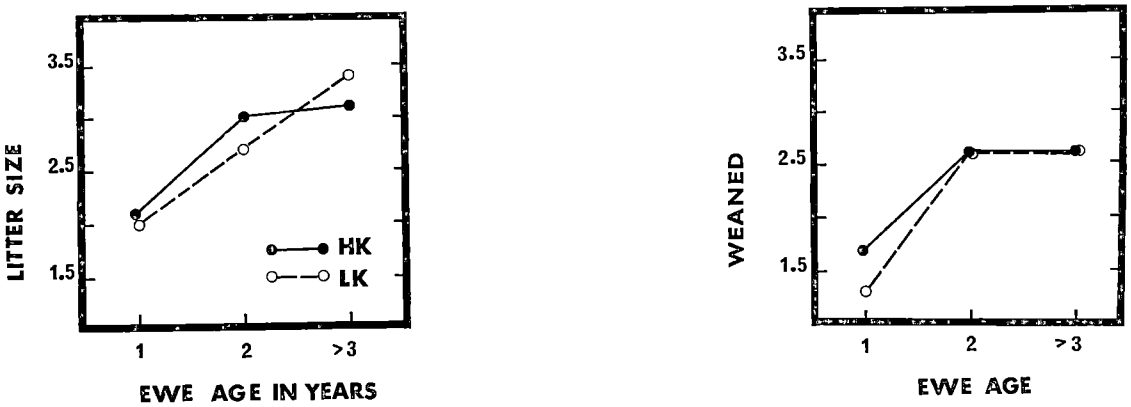


Fig. 15. The relationship between age of ewe and litter size at birth and the number of lambs weaned of ewes of different potassium types.

Table 27. Means and standard errors of reproduction and production characters of ewes of different potassium phenotypes.

Ewe K+ type	No. of ewes	Body weight kg	Wool weight	Litter size	Weaned	No. of lambs	Haematocrit value	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
		$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
HK	274	60,69±0,77	2,68±0,05	2,9±0,06	2,4±0,16†	791 (381) *	33,20±0,19	2,67±0,03	3,33±0,04	6,53±0,09	11,04±0,15	14,13±0,19	26,91±0,26	31,68±0,45
LK	54	66,78±0,99	2,85±0,10	3,1±0,25	2,4±0,15	140 (78) *	33,83±0,38	2,52±0,07	3,21±0,08	6,43±0,15	11,02±0,15	14,18±0,35	27,54±0,65	32,44±0,88

† significant at 5 % level.
* the number in parenthesis is for lambs at different ages.

Table 28. Means and standard errors of reproduction and production characters of ewes of different potassium phenotypes in different regions.

Region	Ewe K+ type	No. of ewes	Body weight kg	Wool weight	Litter size	Weaned	No. of lambs	Haematocrit value	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
			$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
East	HK	127	53,24±1,04	2,57±0,06	3,0±0,09	2,5±0,19	381	32,30±0,21	2,67±0,03	3,11±0,05	6,53±0,09	11,04±0,15	14,13±0,19	25,98±0,39	31,68±0,45
	LK	26	61,61±1,22	2,64±0,12	3,4±0,19†	2,7±0,20	78	33,41±0,43	2,52±0,07	3,04±0,09	6,43±0,15	11,02±1,25	14,18±0,35	26,89±0,82	32,44±0,89
South	HK	147	62,87±0,84	2,53±0,07	2,7±0,09	2,3±0,07	410	35,28±0,30	—	3,47±0,06	—	—	—	27,73±0,34	—
	LK	28	67,83±1,26	2,92±0,19	2,8±0,22	2,2±0,12	62	35,27±0,74	—	3,38±0,12	—	—	—	28,39±1,03†	—

† significant at 5 % level.

Table 29. Means and standard errors of reproduction and production characters of rams of different potassium phenotypes.

Ram K+ type	No. of ewes mated	Litter size	Weaned	No. of lambs	Haematocrit value	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
		$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
HK	202	3,0±0,08	2,5±0,07	597	33,89±0,24	2,56±0,05	3,45±0,05	6,50±0,13	11,09±0,23	14,27±0,27	27,79±0,29†	32,14±0,63
LK	103	3,1±0,10	2,7±0,09	316	32,96±0,30	2,71±0,05	3,29±0,05	6,47±0,12	11,04±0,21	13,98±0,27	25,84±0,49	31,82±0,61

† significant at 5 % level.

Table 30. Means and standard errors of reproduction and production characters of different potassium mating types in different regions.

Region	Phenotype of parents	No. of sires	No. of ewes	No. of lambs	Litter size	Weaned	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
	Sire × dam				$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
East	HK × HK..	3	69	125	3,1±0,17	2,4±0,18	2,58±0,05	3,03±0,08	6,56±0,15	11,21±0,27	14,42±0,31	26,48±0,63	32,19±0,75
	HK × LK..	2	13	30	3,1±0,14	2,7±0,29	2,54±0,08	3,07±0,12	6,31±0,17	10,79±0,40	13,95±0,58	28,78±1,32†	33,39±1,27
	LK × LK..	4	12	35	3,4±0,32†	2,6±0,31	2,61±0,12	3,13±0,12	6,70±0,28	11,63±0,41	14,88±0,59	27,65±1,28	33,86±1,45
	LK × HK..	4	51	161	3,0±0,13	2,6±0,12	2,74±0,06	3,11±0,08	6,36±,015	10,80±0,25	13,78±0,32	25,38±0,63	31,23±0,71
South	HK × HK..	7	153	364	2,7±0,10	2,3±0,08	—	3,57±0,06	—	—	—	27,91±0,37	—
	HK × LK..	6	22	50	2,8±0,23	2,2±0,23	—	3,42±0,13	—	—	—	29,12±1,04†	—

† significant at 5 % level.

Table 31. Lamb mortality of different ages with regard to different ewe potassium phenotypes in different regions.

Ewe K+ type	No.	Eastern region												Southern region												Total											
		No. of lambs born		Born alive		Still-born		0—3 days		4—14 days		14 days—4 months		No. of lambs born		Born alive		Still-born		0—3 days		4—14 days		14 days—4 month		No. of lambs born		Born alive		Still-born		0—3 days		4—14 days		14 days—4 months	
	%	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
HK	No.	181	182	164	152	8	15	1	8	4	2	4	5	202	203	173	168	12	13	9	13	2	5	6	4	383	386	337	321	20	28	10	21	6	7	10	9
	%			90,6	83,5	4,4	8,2	0,6	4,4	2,2	1,1	2,2	2,8			85,6	82,8	5,9	6,4	4,5	6,4	1,0	2,5	3,0	2,0			88,0	83,2	5,2	7,3	2,6	5,4	1,6	1,8	2,6	2,3
LK	No.	46	30	38	25	4	3	2	2	0	0	2	0	27	32	20	27	1	1	2	2	3	1	1	1	73	62	58	52	5	4	4	4	3	1	3	1
	%			82,6	83,3	8,7	1,0	4,4	6,7	0,0	0,0	4,4	0,0			74,0	84,4	3,7	3,1	7,4	6,3	11,1	3,1	3,7	3,1			79,5	83,9	6,9	6,5	5,5	6,5	4,1	1,6	4,1	1,6

Table 32. Lamb mortality at different ages with regard to different ram potassium phenotypes in different regions.

Ram K+ type	No.	Eastern region												Southern region												Total											
		No. of lambs born		Born alive		Still-born		0—3 days		4—14 days		14 days—4 months		No. of lambs born		Born alive		Still-born		0—3 days		4—14 days		14 days—4 months		No. of lambs born		Born alive		Still-born		0—3 days		4—14 days		14 days—4 months	
	%	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
HK	No.	77	75	67	62	5	8	1	1	1	1	3	3	211	222	177	177	12	13	10	15	5	6	7	11	288	292	244	240	17	21	11	16	6	7	10	8
	%			87,0	82,7	6,5	10,7	1,3	1,3	1,3	1,3	3,9	4,0			83,9	79,7	5,7	5,9	4,7	6,8	2,4	2,7	3,3	5,0			847	822	59	72	38	55	21	24	35	27
LK	No.	150	155	140	128	4	6	3	15	1	2	2	4	1	—	1	—	0	—	0	—	0	—	0	—	152	155	141	128	4	6	4	15	1	2	2	4
	%			93,3	85,6	2,7	3,9	2,0	9,7	0,7	1,3	1,3	2,6			10,0	—	0,0	—	0,0	—	0,0	—	0,0	—			92,8	82,6	2,6	3,9	2,6	9,9	0,7	1,3	1,3	2,6

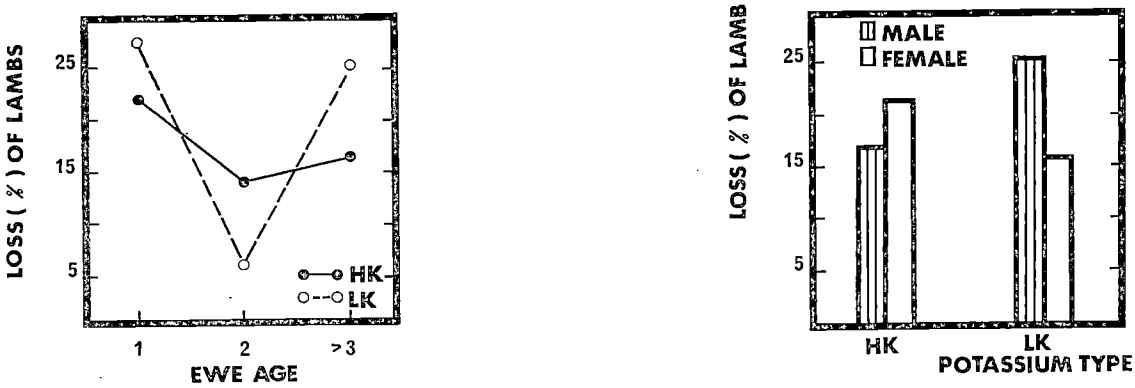


Fig. 16. Lamb mortality in relation to age of ewe and sex of lamb of ewes of different potassium types.

phenotypes of ewes in both regions. In most cases heterozygous ewes (LK) were better than homozygous (HK) as far as the number of lambs born per ewe mated is concerned. (In the eastern region 3,4 vs 3,0 lambs born($P < 0,05$) and in the southern region the figure was 2,8 vs 2,7 lambs born). HK ewes did better than LK ewes in terms of the number of lambs weaned. These differences were significant ($P < 0,05$). The rate of quintuplets and quadruplets was higher for LK ewes but the cases of ewes with triplets were less frequent among LK ewes than among HK ewes. Twinning rate was again higher for LK ewes.

As regards the performance of rams it can again be seen that LK rams were better than HK rams (Table 29), giving +0,1 more lambs born and +0,2 more lambs weaned per ewe mated than the HK rams. However, the differences were not significant.

Table 30 gives the number of lambs born and weaned per ewe mated from each mating type. LK ♂ × LK ♀ gave the highest figure for lambs born. The differences were significant at the 0,05 level. LK ewes did on average better than the homozygotes, giving +0,2 more lambs born.

3.2.3.3.1. Lamb mortality

Lamb losses at birth, from birth to 3 days, from 4—14 days and from 14 days to 4 months are given in Tables 31 and 32 and Figure 16. Mortality refers to stillbirth, death and disappearance.

From Table 31 it can be seen that the percentage of lambs dead at different ages, for each ewe potassium type, varied between regions. It appeared that losses of LK phenotypes were higher than losses of HK phenotypes (18,5 % vs 14,4 %). The difference was significant ($P < 0,05$).

Mortality of lambs according to the sex for the potassium type of the ewe in the different regions showed that the majority of deaths, 20,6 %, occurred in the male lambs of ewes with LK phenotype ($P < 0,05$).

Regarding sire potassium types (Table 32), a striking result was the mortality (16,6 %) of the HK phenotypes compared to that of the LK phenotypes (12,4 %). However, the differences between types seldom approached the level of significance. The highest mortality occurred in the female lambs of rams with HK phenotypes; however, the differences were not significant.

3.2.3.4. Production characters

3.2.3.4.1. Ewe body weight and wool weight

The mean values with their standard errors for the two regions are given in Tables 27 and 28 and Figure 17. The differences attributed to

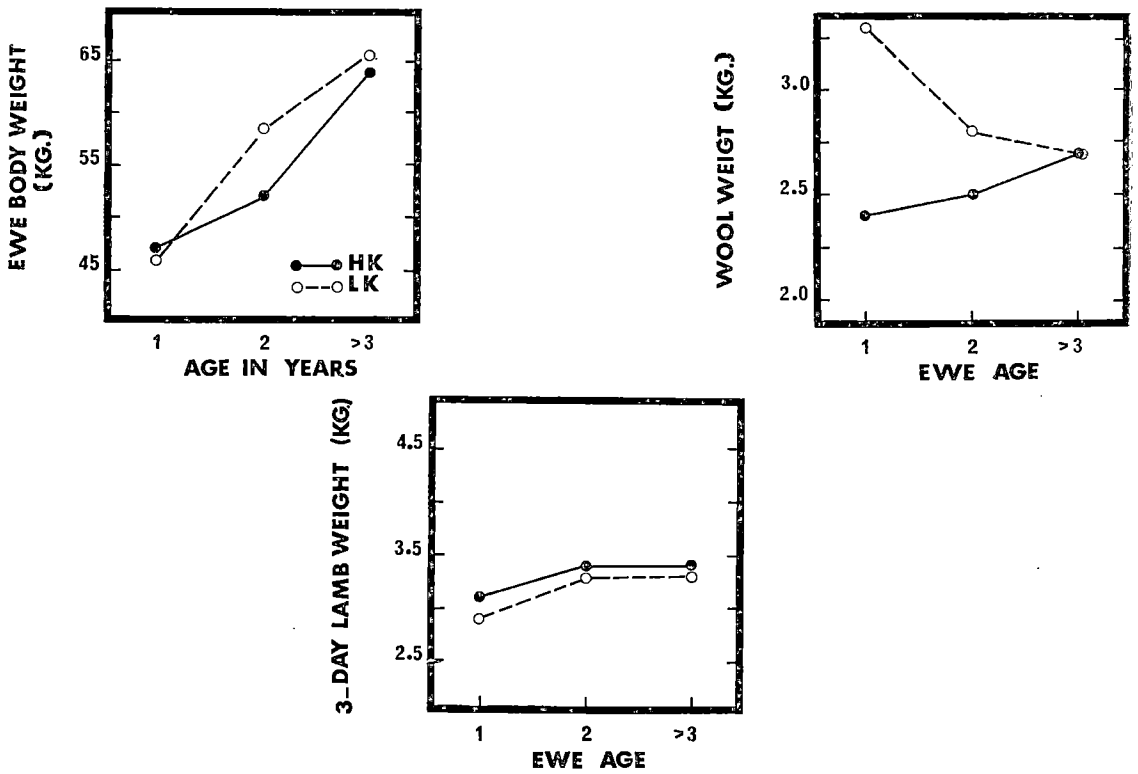


Fig. 17. The relationship between age of ewe and ewe body weight, wool weight and 3-day lamb weight with respect to ewe potassium type.

potassium types were rarely significant at accepted levels of probability. However, the body weight of ewes LK phenotype showed a large superiority over that of ewes of HK phenotype (67 kg vs 61 kg). The results of wool weight show that sheep of LK type produced more wool than sheep of HK type, though not significantly so.

3.2.3.4.2. Lamb weight at three days

The means for the lamb weights corresponding to ewe potassium types (Tables 27 and 28 and Figure 17) show only small variations. Lambs of ewes with HK phenotype were only marginally better than lambs of LK phenotypes. As regards the potassium type of the ram (Table 29), no marginal superiority as to lamb weight was seen, and the difference between the two phenotypes was small, and in favour of HK type (3,451 vs 3,285 kg). Table 30 shows the lamb weight from each mating type. HK ♂ × HK ♀ gave the highest figures for lamb weight in the southern region compared to the other observed mating type, which was HK ♂ × LK ♀ (3,572 kg vs 3,418 kg), whereas LK ♂ × LK ♀ did better than the other mating types in the eastern region (3,125 vs 3,069 kg). However, these differences were not significant.

Regarding lamb phenotypes and their association with the 3-day weight (Tables 33 and 34), individuals with HK phenotypes were slightly heavier than those with LK phenotypes. Female lambs with HK type were +0,155 kg heavier than female lambs with LK type. However, no differences between male lambs occured according to their potassium types. When birth type of lambs was considered (Table 34) the differences generally favoured HK phenotypes.

Table 33. Means and standard errors of weight (kg) of lambs of different potassium phenotypes and sexes.

Lamb K^+ type	Lamb sex	No. of lambs	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
			$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
HK	Male	168	2,74±0,06	3,24±0,07	6,71±0,14	11,30±0,23	14,57±0,29	29,33±0,43††	36,09±0,65††
	Female ..	157	2,64±0,05	3,09±0,07	6,14±0,14	10,42±0,26	13,48±0,29	23,32±0,44	26,78±0,42
LK	Male	45	2,74±0,10	3,30±0,15	6,52±0,24	11,30±0,44	14,62±0,57	29,56±1,01††	36,37±1,07††
	Female ..	48	2,56±0,09	2,93±0,13	6,09±0,18	10,36±0,31	13,19±0,40	23,12±0,64	27,30±0,60
Total	HK	325	2,70±0,04	3,17±0,05	6,45±0,10	10,91±0,17	14,08±0,21	26,46±0,35	31,91±0,52
	LK	93	2,66±0,07	3,11±0,10	6,32±0,15	10,87±0,28	13,91±0,36	26,30±0,68	32,12±0,81

†† significant at 1 % level.

Table 34. Means and standard errors of weights (kg) of lambs of different potassium phenotypes according to birth type.

Birth type	K^+ type	No. of lambs	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
			$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
Single ...	HK	27	2,96±0,36	4,40±0,29†	8,08±0,91†	12,97±1,35	15,93±1,58†	32,44±1,22†	35,67±2,17†
	LK	10	2,31±0,21	3,53±0,48	8,00±0,89	12,11±1,57	14,79±1,34	32,01±1,62	34,51±2,11
Twins ...	HK	153	3,01±0,10	3,80±0,08	7,71±0,21†	12,46±0,32	15,57±0,42†	28,71±0,52	34,54±1,27†
	LK	27	2,81±0,18	3,34±0,16	7,20±0,23	12,33±0,37	15,61±0,63	27,58±1,37	31,50±1,77
Triplets..	HK	291	2,71±0,06	3,18±0,06	6,56±0,12	11,02±0,24	14,10±0,29	26,69±0,41	31,51±0,64
	LK	43	2,54±0,11	3,23±0,12	6,43±0,20	10,91±0,34	13,97±0,49	27,19±1,21	32,30±1,48
Quad-ruplets	HK	215	2,56±0,05	3,11±0,06	6,25±0,15	10,93±0,28	14,14±0,32	25,86±0,51	32,24±0,83
	LK	53	2,44±0,09	3,11±0,12	6,29±0,23	10,86±0,42	14,40±0,54	27,73±1,02	34,06±1,50†
Quintu-plet	HK	105	2,45±0,06	3,02±0,09	5,61±0,20	9,62±0,32	12,61±0,48	24,80±0,77	27,63±1,09
	LK	15	2,27±0,18	2,90±0,23	5,77±0,64	10,16±0,91	11,87±0,96	26,54±1,39	27,68±2,24

† significant at 5 % level.
†† significant at 1 % level.

3.2.3.4.3. Weaning weight of lambs

Tables 27 and 28 give the mean values for 4-month lamb weights of ewes having different potassium types. There were small differences between types, with the exception of the LK phenotypes which gave heavier lambs at 4-months than HK phenotypes (27,541 kg vs 26,914 kg). This difference was not, however, significant. The differences observed were most probably due to sampling errors.

From Table 29 is apparent that lambs sired by rams of LK phenotypes were inferior in weight ($P < 0,05$) to lambs sired by HK phenotypes (25,843 kg vs 27,786 kg). It is interesting to note that HK ♂ × LK ♀ mating type (Table 30) gave the highest 4-month lamb weight ($P < 0,05$), but on average, LK ewes did better than homozygous ones, giving 2,28 kg and 1,21 kg more in the eastern and southern regions respectively.

As regards lamb phenotypes (Tables 33 and 34), one can see that male lambs with LK phenotype were slightly heavier at 4-months than male lambs of HK phenotype. The vice versa was noted for female lambs. Within potassium type male lambs were significantly ($P < 0,01$) heavier than female lambs. According to lamb birth type (Table 34) we see that the differences were generally in favour of LK phenotypes.

3.2.3.4.4. Weights of lambs at different ages

The mean weights of lambs at birth, three weeks, six weeks, eight weeks and five months are given according to the phenotype of the dam in Tables 27 and 28, according to the phenotype of the sire in Table 29, according to the mating type in Table 30 and according to the phenotype of the lamb itself in Tables 33 and 34.

Table 35. The frequency distribution of glutathione phenotypes and the gene frequencies of high and low glutathione levels in different regions.

Region	No. of animals	Glutathione phenotypes %		Gene frequency		Latitudes	Meters above the sea level
		GSH High	GSH Low	GSH^H	GSH^h		
East	453	50,55	49,45	0,51	0,49	62°	100
South	307	61,24	38,76	0,61	0,39	60°	45
Total	760	54,87	45,13	0,55	0,45		

Table 36. Distribution of glutathione phenotypes in the offspring from four different matings.

Phenotype of parents Sire × dam	No. of sires	No. of dams	Eastern region			No. of sires	No. of dams	Southern region			No. of sires	No. of dams	Total		
			GSH type of offspring					GSH type of offspring					GSH type of offspring		
			GSH^H	GSH^h	Total			GSH^H	GSH^h	Total			GSH^H	GSH^h	Total
$GSH^H \times GSH^H$	5	51	74	26	100	4	72	20	7	27	9	123	94	33	127
$GSH^H \times GSH^h$	5	39	62	23	85	4	18	8	16	24	9	57	70	39	109
$GSH^h \times GSH^h$	2	13	0	32	32	3	22	3	26	29	5	35	3	58	61
$GSH^h \times GSH^H$	2	25	30	46	76	3	54	49	76	125	5	79	79	122	201
Total	14	128	166	127	293	14	166	80	125	205	28	294	246	252	498

The phenotype of the dam had no statistically significant effect on the lamb weights at any of the five ages, although there was a variation between the types. As regards birth weight, three week and six week weights, ewes of HK type had the heaviest lambs, whereas LK ewes had the heaviest lambs at eight weeks and five months, but when the age of the ewe was taken into consideration the LK type seemed to give the best result for one- and two-year old ewes at three, six and eight weeks, but the difference was no longer clear for the three-year old ewes.

Sires of LK type had the heaviest offspring at birth, but at all the other ages sires of HK type were the best. None of the differences, however, was statistically significant. The mating type LK ram × HK ewe gave the heaviest lambs at birth, whereas LK ram × LK ewe matings had the best result at the other four ages. The differences between lamb phenotypes were not statistically significant. However, the HK type seemed to be the heavier at all the ages other than five months, the age at which LK lambs were slightly heavier.

3.2.4. Glutathione

3.2.4.1. Glutathione types

The erythrocyte reduced glutathione (GSH) level in whole blood was determined spectrophotometrically according to the method of Beutler et al. (1963), which measures only GSH and not GSSG. The GSSG is a minor portion. Each animal was classified according to glutathione concentration. Those sheep with GSH value below 55 mg per 100 ml packed red cells were classified as GSH-low type (GSH^h), and those with values above this as GSH-high type (GSH^H) (Tucker and Kilgour, 1970).

3.2.4.2. Distribution of glutathione types

The distribution of animals according to GSH type in the two regions is given in Table 35 and Figure 18, and it is apparent from the data that the GSH-high type was predominant among the sheep in southern Finland (60 % vs 40 %), whereas among the sheep in eastern

Table 37. Erythrocyte GSH levels in two groups of phenotypically high-GSH type sheep, one of which is known to be all heterozygotes and the other of which is presumed to be a mixture of heterozygotes.

Mean erythrocte GSH (mg/100 ml ± SE)				
Phenotype of parents Sire × dam	No. of animals	High—GSH parental mean	No. of animals	Offspring
$GSH^H \times GSH^H$	74	102,3±1,25	74	93,4±2,05 †
$GSH^H \times GSH^h$	47	108,5±3,12 NS	47	79,3±2,14 †

† significant at 1 % level.
NS = not significant.

Finland the differences in the distribution of GSH-high and low types were very small (50,55% vs 49,45 %).

Table 36 presents inheritance data for the Finnsheep. The lambs were tested when they were at least 3 months old and matings between GSH-high × GSH-high types resulted in both GSH-high and GSH-low type offspring, whereas GSH-low × GSH-low matings produced only GSH-low type lambs. The only notable discrepancy was the occurrence of the three GSH-high animals in southern Finland from matings of GSH-low parents, and these can probably be attributed to erroneous identity of the progeny.

Table 38. Mean erythrocyte GSH concentration within glutathione phenotype.

Phenotype	No. of animals	Mean erythrocyte GSH (mg/100 ml ± SE)
GSH^H	219	75,11±1,04
GSH^h	100	37,87±1,29

3.2.4.3. Reproductive performance

The number of lambs born and weaned from both known parents showed a considerable variation in the two regions (Table 39 and Figure 19). GSH^H type ewes were found to produce and wean more lambs than GSH^h type ewes in both regions. However, the differences were significant only for the number of lambs weaned ($P < 0,05$). The distribution of litter sizes shows that GSH^H ewes gave most of the litters with twins and quintuplets, but not with triplets nor quadruplets. The maximum litter size was reached by 3-year old ewes of GSH^h type (3,4 ± 0,132). As for the performance of rams (Table 40) we see that GSH^h type rams were better than GSH^H type rams. However, the differences were not significant. The GSH^h rams gave +0,2 and +0,1 more lambs born in the eastern and southern regions respectively, but weaned fewer of them than did GSH^H type rams. Mating of GSH^h rams to GSH^H ewes (Table 41) in southern Finland resulted in litters which gave +0,1 lambs more than mating of GSH^h rams to GSH^h ewes. In eastern Finland the number of lambs born from matings between rams of both GSH-types and ewes of GSH^h type was larger ($P < 0,05$) than that from other mating types, giving +0,2 more lambs, but on average GSH^H ewes did

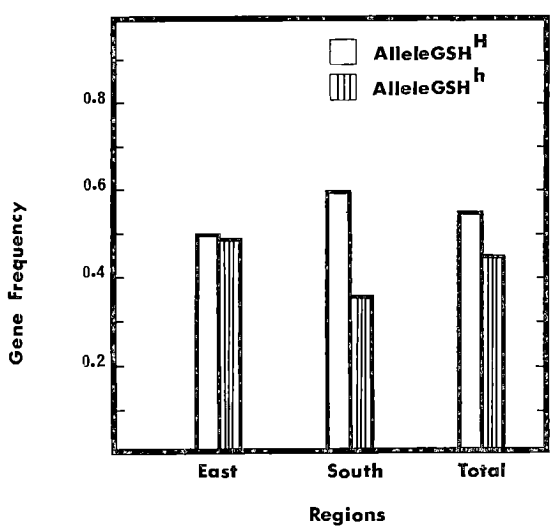


Fig. 18. The frequency of the high-glutathione (GSH^H) and low-glutathione (GSH^h) alleles in different regions of Finnsheep.

Table 39. Means and standard errors of reproduction and production characters of ewes of different glutathione phenotypes.

Region	Ewe GSH type	No. of ewes	Body weight kg	Wool weight	Litter size	Weaned	No. of lambs	Heamatocrit value	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
			$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
Total	GSH^H	228	59,02±0,86	2,58±0,05	2,9±0,18	2,5±0,15†	629	33,62±0,21	2,65±0,04	3,32±0,04	6,66±0,10	11,41±0,17†	14,55±0,21†	26,93±0,29	32,42±0,51
	GSH^h	100	56,47±1,27	2,59±0,07	2,7±0,23	2,2±0,12	306	32,89±0,27	2,64±0,04	3,33±0,08	6,26±0,12	10,42±0,21	13,22±0,26	27,20±0,44	30,83±0,63
East	GSH^H	95	54,62±1,30	2,55±0,07	3,0±0,10	2,6±0,11	228	33,08±0,25	2,65±0,04	3,10±0,05	6,67±0,10	11,42±0,17	14,55±0,21	25,97±0,42	32,45±0,51
	GSH^h	58	54,82±1,43	2,64±0,07	2,8±0,13	2,3±0,12	170	31,64±0,28	2,64±0,04	2,93±0,12	6,25±0,25	10,38±0,21	13,51±0,26	26,38±0,61	30,74±0,63
South	GSH^H	133	63,57±0,87	2,61±0,07	2,8±0,10	2,4±0,08	340	34,87±0,38	—	3,51±0,06	—	—	—	27,70±0,38	—
	GSH^h	42	62,71±1,55	2,33±0,14	2,6±0,15	2,1±0,14	136	35,69±0,40	—	3,35±0,09	—	—	—	28,21±0,68	—

† significant at 5 % level.

Table 40. Means and standard errors of reproduction and production characters of rams of different glutathione phenotypes.

Region	Ram GSH type	No. of ewes mated	Litter size	Weaned	No. of lambs	Heamatocrit value	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
			$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
Total	GSH^H	207	2,8±0,07	2,4±0,08	588	33,46±0,26	2,68±0,04	3,43±0,04	6,50±0,11	10,93±0,19	13,95±0,24	26,68±0,30	31,72±0,55
	GSH^h	98	2,9±0,11	2,3±0,11	285	33,68±0,28	2,55±0,05	3,33±0,06	6,45±0,14	11,26±0,27	14,54±0,31	28,30±0,44	32,72±0,71
East	GSH^H	117	2,9±0,09	2,5±0,09	359	32,58±0,27	2,68±0,04	3,27±0,05	6,50±0,11	10,93±0,19	13,95±0,24	25,83±0,45	31,72±0,55
	GSH^h	36	3,1±0,16	2,5±0,20	119	32,85±0,40	2,58±0,05	3,04±0,08	6,26±0,14	11,26±0,27	14,54±0,31	27,38±0,65†	32,73±0,71
South	GSH^H	90	2,7±0,12	2,3±0,11	251	36,71±0,48	—	3,60±0,07	—	—	—	27,57±0,40	—
	GSH^h	62	2,8±0,14	2,2±0,12	183	34,68±0,35	—	3,45±0,08	—	—	—	28,92±0,59	—

† significant at 5 % level.

Table 41. Means and standard errors of reproduction and production characters of different mating types of different glutathione phenotypes in different regions.

Region	Phenotype of parents	No. of sires	No. of ewes	No. of lambs	Litter size	Weaned	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
	Sire × dam				$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
East	$GSH^H \times GSH^H$	5	51	159	3,0 ±0,14	2,5 ±0,14	2,69 ±0,06	3,13 ±0,07	6,60 ±0,15	11,27 ±0,23	14,33 ±0,30	25,97 ±0,63	32,49 ±0,63
	$GSH^H \times GSH^h$	5	39	80	3,2 ±0,17	2,6 ±0,15	2,66 ±0,07	2,76 ±0,17	6,15 ±0,19	10,26 ±0,34	13,30 ±0,42	25,52 ±0,84	30,22 ±0,85
	$GSH^h \times GSH^h$	2	13	43	3,2 ±0,24†	2,6 ±0,27	2,50 ±0,09	2,97 ±0,18	6,18 ±0,22	10,61 ±0,42	14,00 ±0,54	28,48 ±1,23†	31,81 ±1,27
	$GSH^h \times GSH^H$	2	25	69	3,1 ±0,21	2,5 ±0,28	2,63 ±0,06	3,05 ±0,08	6,70 ±0,17	11,64 ±0,34	14,87 ±0,39	26,72 ±0,77	33,27 ±0,91
South	$GSH^H \times GSH^H$	4	72	198	2,8 ±0,13	2,4 ±0,12	—	3,73 ±0,08	—	—	—	27,50 ±0,46	—
	$GSH^H \times GSH^h$	4	18	46	2,5 ±0,23	2,1 ±0,18	—	3,17 ±0,14	—	—	—	27,86 ±0,84	—
	$GSH^h \times GSH^h$	3	22	63	2,7 ±0,24	2,2 ±0,25	—	3,65 ±0,12	—	—	—	30,50 ±0,93†	—
	$GSH^h \times GSH^H$	3	54	107	2,8 ±0,18	2,2 ±0,14	—	3,31 ±0,10	—	—	—	27,78 ±0,80	—

† significant at 5 % level.

better than GSH^h ewes, giving on average +0,1 more lambs weaned. In general, the number of lambs weaned was +0,1 higher from GSH^H ♂ × GSH^H ♀ matings than from the other mating types.

3.2.4.3.1. Lamb mortality

Losses in lambs at birth and from birth to 3 days, 4—14 days and from 14 days to 4 months are given in Tables 42 and 43 and correspondingly in Figure 20. The percentage of lambs dead at different ages according to ewe glutathione type varied from region to region, and it appeared that the losses were higher for ewes of GSH^h phenotype than for ewes of GSH^H phenotype (18,5 % vs 17,5 %), though not significantly so. As regards the percentage of stillbirths, GSH^h ewes suffered greater losses (12,7 %) than GSH^H ewes (8,2 %). The differences among phenotypes were significant at the 0,05 level of probability.

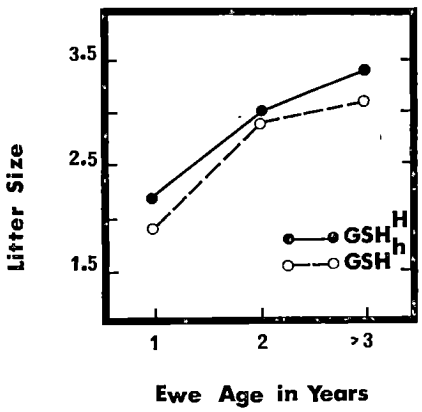
As far as the mortality of lambs of ewes of both glutathione types according to the sex of the lambs is concerned, most of the lamb losses occured in the female lambs of ewes having GSH^h phenotype. The range varied from 8,9 % for males to 21 % for females ($P < 0,01$).

Regarding sire glutathione types a noticeable result was the high mortality (22,2 %) of the GSH^h phenotype compared to that of the other type (15,8 %). Extract from the analysis of variance show that the differences were attributable to glutathione type and were significant at the 0,05 level of probability. Once again, male lambs of both phenotypes GSH^H and GSH^h seemed to have some advantage over the corresponding females.

3.2.4.4. Production characters

3.2.4.4.1. Ewe body weight and wool weight

Average values for ewe body weight and wool weight for each glutathione type are presented in Table 39 and correspondingly in Figure 21.



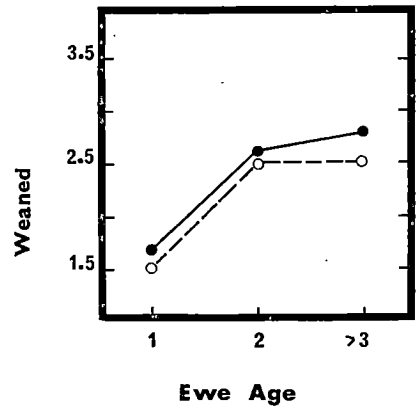
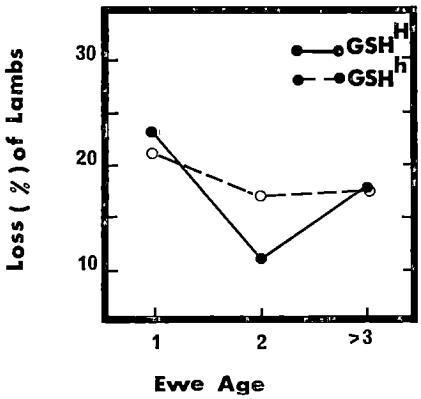


Fig. 19. The relationship between age and litter size and the number of lambs weaned of ewes of different glutathione type.



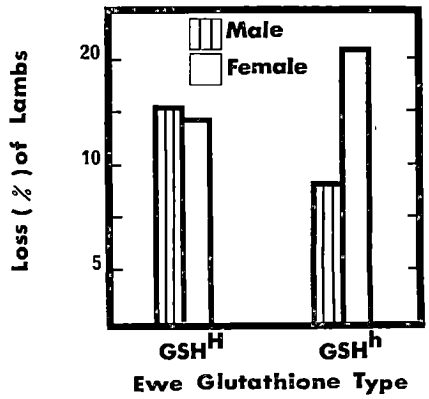
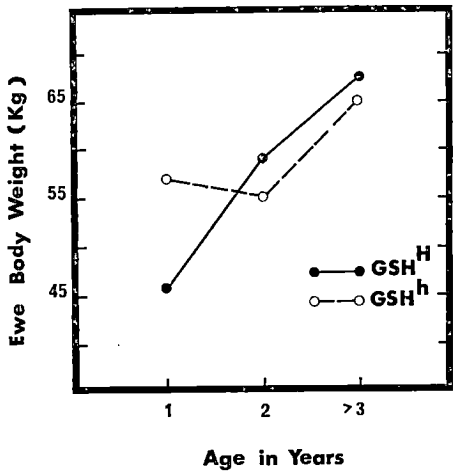


Fig. 20. Lamb mortality in relation to age of ewe and lamb sex and different glutathione type of the ewe.



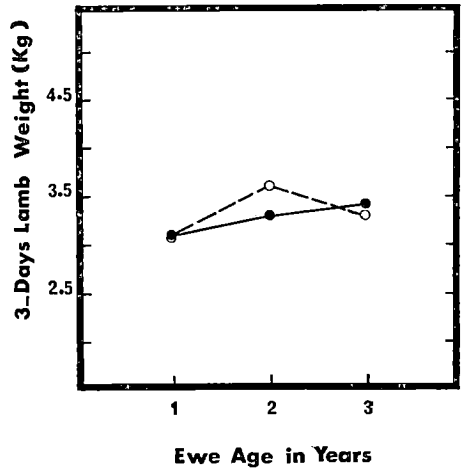


Fig. 21. The relationship between age of ewe and ewe body weight and 3-day lamb weight according to different glutathione types.

Table 42. Lamb mortality of ewes of different glutathione phenotypes according to the sex and age of lambs.

Ewe GSH type	No.	Eastern region												Southern region												Total											
		No. of lambs born		Born alive		Still-born		0—3 days		4—14 days		14 days—4 months		No. of lambs born		Born alive		Still-born		0—3 days		4—14 days		14 days—4 months		No. of lambs born		Born alive		Still-born		0—3 days		4—14 days		14 days—4 months	
	%	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
GSH^H	No.	142	136	124	113	10	12	2	7	3	1	3	3	156	179	127	155	11	7	11	9	4	5	3	3	298	316	251	269	21	19	13	16	7	6	6	6
	%			87,3	83,1	7,0	8,8	1,4	5,2	2,1	0,7	2,1	2,2			81,4	86,6	7,1	3,9	7,1	5,0	2,6	2,8	1,9	1,7			84,2	85,1	7,1	6,0	4,4	5,1	2,4	1,9	2,0	1,9
GSH^h	No.	85	76	78	64	2	6	1	3	1	1	3	2	73	60	66	43	2	8	0	6	1	1	4	2	158	136	144	107	4	14	1	9	2	2	7	4
	%			91,8	84,2	2,4	7,9	1,2	4,0	1,2	1,3	3,5	2,6			90,4	71,7	2,7	13,3	0,0	10,0	1,4	1,7	5,5	3,3			91,1	78,7	2,5	10,3	0,6	6,6	1,3	1,5	4,4	2,9

Table 43. Lamb mortality of rams of different glutathione phenotypes according to the sex and age of lambs.

Ram GSH type	No.	Eastern region												Southern region												Total											
		No. of lambs born		Born alive		Still-born		0—3 days		4—14 days		14 days—4 months		No. of lambs born		Born alive		Still-born		0—3 days		4—14 days		14 days—4 months		No. of lambs born		Born alive		Still-born		0—3 days		4—14 days		14 days—4 months	
	%	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
GSH^H	No.	174	175	158	147	8	6	3	15	2	2	3	5	119	129	105	105	5	7	5	9	1	4	3	4	293	305	263	253	13	13	8	24	3	6	6	9
	%			90,8	84,0	4,6	3,4	1,7	8,6	1,2	1,1	1,7	2,9			88,2	81,4	4,2	5,4	4,2	7,0	0,8	3,1	2,5	3,1			89,8	83,0	4,4	4,3	2,7	7,9	1,0	2,0	2,1	3,0
GSH^h	No.	53	55	49	43	1	8	1	1	0	1	2	2	94	87	73	72	7	6	6	6	4	2	4	1	147	142	122	115	8	14	7	7	4	3	6	3
	%			92,5	78,2	1,9	14,6	1,9	1,8	0,0	1,8	3,8	3,6			77,7	82,8	7,5	6,9	6,4	6,9	4,3	2,3	4,3	1,2			83,0	81,0	5,4	9,9	4,8	4,9	2,7	2,1	4,1	2,1

Table 44. Means and standard errors of weight (kg) of lambs of different glutathione phenotypes and different sexes.

Lamb GSH type	Lamb sex	No. of lambs	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
			$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
GSH^H	Male	88	2,62±0,07	3,05±0,11	6,45±0,19	11,02±0,30	14,18±0,39	28,69±0,71†	35,07±0,82
	Female	92	2,70±0,07	3,26±0,11	6,27±0,20	10,78±0,41	13,83±0,42	24,54±0,57	27,34±0,55
GSH^h	Male	125	2,84±0,06	3,35±0,08	6,84±0,16	11,56±0,27	14,94±0,34	29,87±0,46††	37,14±0,73†
	Female	113	2,58±0,06	2,92±0,07	6,04±0,13	10,17±0,62	13,13±0,28	22,26±0,47	26,68±0,45
Total	GSH^H	180	2,65±0,05	3,17±0,08	6,38±0,14	10,92±0,24	14,04±0,29	26,60±0,48	31,96±0,64
	GSH^h	238	2,71±0,05	3,15±0,05	6,45±0,11	10,87±0,18	14,03±0,23	26,29±0,41	31,97±0,60

† significant at 5 % level.
†† significant at 1 % level.

There was a slight superiority but not significantly of GSH^H phenotypes over GSH^h phenotypes in ewe body weight in southern Finland (63,57 kg vs 62,71 kg). Data on fleece weight from southern Finland show that GSH^H phenotypes produced more wool than GSH^h phenotypes (2,61 kg vs 2,33 kg). However, extracts from the analysis of variance shows that differences attributable to glutathione type were rarely significant at accepted levels of probability.

3.2.4.4.2. Lamb weight at three days

The means for the lamb weights at three days according to ewe and ram GSH type (Tables 39 and 40 and correspondingly in Figure 21) showed only small differences, which were not significant between types. Table 41 shows that GSH^H ♂ × GSH^H ♀ mating type gave the highest lamb weight in both regions, but on average, GSH^H type ewes did better than GSH^h type ewes, giving lambs which were +0,227 kg and + 0,110 kg heavier in eastern and southern Finland respectively. As regards the association between lamb phenotype and three-day weight (Tables 44 and 45) we note a slight superiority of GSH^H phenotype over GSH^h phenotype. However, differences between glutathione types were observed when type of birth was considered, GSH^H phenotypes being heavier than GSH phenotypes ($P < 0,05$). Similar patterns were revealed when sex of lamb was included. GSH^h male lambs were 0,292 kg heavier than GSH^H male lambs, whereas GSH^H female lambs were the heaviest among female lambs, though not significantly so, the difference being 0,342 kg.

3.2.4.4.3. Weaning weight of lambs

Table 39 gives mean values and standard errors for 4-month lamb weight of ewes having different glutathione types in the two regions. In eastern Finland, the means for the weight showed a small superiority of ewes possessing GSH^h type over ewes possessing GSH^H type (26,383 kg vs 25,968 kg). A similar pattern was apparent in southern Finland; however, none of the differences was significant. Looking more closely at the phenotype of the ram (Table 40), we see that in both regions, lambs sired by GSH^h phenotypes were 1,5 kg heavier than lambs sired by GSH^H phenotypes. It is interesting to note that lambs from GSH^h ♂ × GSH^h ♀ matings were 2,6 kg heavier than the lambs of other mating types. The differences were significant at the 0,05 level.

From Table 44 it can be seen that GSH^h male lambs were 1,0 kg heavier at weaning than male lambs of GSH^H type, whereas female lambs of GSH^H type were 2,0 kg heavier than female lambs of GSH^h type; these differences were significant at the 0,01 levels. As regards birth type of lambs (Table 45) a small difference in favour of GSH^h phenotype was noted in triplets and quadruplets, but it was found not to be significant.

Table 45. Means and standard errors of weight (kg) of lambs of different glutathione phenotypes according to birth type.

Birth type	GSH type	No. of lambs	Birth weight	3-day weight	3-week weight	6-week weight	8-week weight	4-month weight	5-month weight
			$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE
Single	GSH^H	17	3,51±,044†	4,45±0,35	8,36±0,98	13,36±0,95	16,58±1,32†	32,75±1,33	39,04±1,05†
	GSH^h	19	2,90±0,21	4,38±0,23	7,50±0,74	12,25±0,88	15,40±1,09	32,58±1,05	30,65±1,79
Twins	GSH^H	129	2,94±0,11	3,78±0,09	7,79±0,21	12,83±0,33	15,93±0,46†	28,55±0,58	34,31±0,68†
	GSH^h	52	3,05±0,14	3,57±0,12	7,24±0,33	11,50±0,37	14,87±0,52	28,40±0,87	33,29±0,45
Triplets	GSH^H	223	2,62±0,07	3,18±0,06	6,52±0,14	11,15±0,27	14,19±0,33	26,72±0,45	32,24±0,74†
	GSH^h	114	2,77±0,07	3,31±0,15	6,56±0,16	10,79±0,33	13,93±0,42	27,05±0,75	30,72±0,57
Quadruplet	GSH^H	162	2,59±0,06	3,12±0,07	6,61±0,16	11,63±0,29††	15,01±0,36†	25,36±0,57	33,34±0,98†
	GSH^h	106	2,45±0,06	3,01±0,11	5,76±0,20	9,91±0,35	13,13±0,39	27,48±0,73†	31,60±1,04
Quintuplet	GSH^H	98	2,45±0,07	3,01±0,19	5,73±0,24	9,96±0,40	12,91±0,57†	25,65±0,81††	28,03±1,27†
	GSH^h	22	2,37±0,08	2,80±0,38	5,45±0,33	9,19±0,54	11,67±0,68	22,44±1,01	26,85±1,63

† significant at 5 % level.
†† significant at 1 % level.

3.2.4.4.4. Weights of lambs at different ages

The mean weights of lambs at birth, three weeks, six weeks, eight weeks and five months are given according to the glutathione level of the dam in Table 39, according to the GSH level of the sire in Table 40, according to the mating type in Table 41 and according to the GSH level of the lamb itself in Tables 44 and 45.

At all five ages the GSH^H ewes gave the heaviest lambs, but only at six weeks and eight weeks were the differences significant ($P < 0,05$). For three-year-old ewes the difference in eight week lamb weight was highly significant ($P < 0,01$), and in favour of GSH^H type.

At birth and three weeks, lambs sired by GSH^H rams were slightly heavier, but at the more advanced ages lambs sired by GSH^h rams were the heaviest. None of the differences, however, was found to be significant.

At all ages except at birth, mating of GSH^h ram to GSH^H ewe gave the heaviest lambs, although the differences were not significant. Generally speaking, there seemed to be no clear difference in weights of lambs with either GSH-type. Male lambs of GSH^h type were the heaviest at all ages. From three weeks onwards, the male lambs were heavier than the female ones within both GSH types; however the differences were not significant.

3.2.5. The association between the various blood polymorphic characters

3.2.5.1. Haemoglobin and transferrin types in relation to erythrocyte glutathione and potassium concentrations

In view of the association between the blood polymorphic characters, a more critical examination was made of mean glutathione and potassium concentration, and of the haematocrit value in each of the haemoglobin and transferrin types of ewes and lambs. The mean values with their standard errors are included in Tables 46—49. They show that ewes with haemoglobin BB had significantly ($P < 0,01$) more glutathione and lower haematocrit values in their blood than animals with haemoglobin AA and AB (67,93 mg/100 ml vs 63,17 mg/100 ml red cells). AA homozygotes had higher ($P < 0,05$) potassium and haematocrit values than AB and BB animals (95,21 mEq/l vs 91,64 mEq/l red cells). When the levels (high and low) of glutathione and potassium were considered (Table 46) similar patterns were found. This poses the question as to whether such differences reflect variation in erythrocyte number in the three types, or differences in glutathione and potassium concentration in red cells containing different haemoglobins.

Table 46. Glutathione and potassium concentrations and haematocrit values in the whole blood of Finnsheep of different haemoglobin, glutathione and potassium types.

Ewe Hb type	No. of ewes	GSH^H mg/100 ml RC	Haematocrit (%)	No. of ewes	GSH^h mg/100 ml RC	Haematocrit (%)	No. of ewes	HK mEq/1 RC	Haematocrit (%)	No. of ewes	LK mEq/1 RC	Haematocrit (%)
		$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$
AA	138	74,13±1,38	34,34±0,29†	56	37,24±1,87	35,34±0,43	163	105,51±1,20†	34,42±0,26	31	41,03±1,58†	35,75±0,62
AB	70	77,16±1,74††	33,25±0,38	42	39,03±1,76	34,24±0,53	98	101,79±1,44	33,48±0,33	14	41,49±1,09	34,58±0,88
BB	19	75,31±1,91	32,13±0,92	10	31,05±1,88	33,00±0,95	19	99,72±1,93	32,68±0,96	10	35,60±2,01	30,25±1,05

† significant at 5 % level.
†† significant at 1 % level.

Table 47. Glutathione and potassium concentrations and haematocrit values in the whole blood of lambs of different haemoglobin types.

Lamb Hb type	No. of lambs	GSH^H mg/100 ml RC	Haematocrit (%)	No. of lambs	GSH^h mg/100 ml RC	Haematocrit (%)	No. of lambs	HK mEq/1 RC	Haematocrit (%)	No. of lambs	LK mEq/1 RC	Haematocrit (%)
		$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$
AA	125	76,26±1,43†	32,63±0,31	136	38,31±1,22†	33,72±0,29	192	112,68±1,05†	33,19±0,25	69	39,85±1,14	33,24±0,53
AB	42	70,68±2,30	33,85±0,58	88	34,35±1,46	33,86±0,36	111	105,66±1,58	33,69±0,33	29	42,06±1,68†	34,82±0,77
BB	23	74,39±1,38	31,49±0,67	24	28,05±1,46	33,49±0,56	28	97,60±1,80	32,22±0,44	10	28,64±1,59	33,86±1,01

† significant at 5 % level.
†† significant at 1 % level.

Table 48. Glutathione and potassium concentrations and haematocrit values of Finnsheep of different transferrin and glutathione and potassium types.

Ewe Tf type	No. of ewes	GSH^H mg/100 ml RBC	Haematocrit (%)	No. of ewes	GSH^h mg/100 ml RBC	Haematocrit (%)	No. of ewes	HK mEq/1 RBC	Haematocrit (%)	No. of ewes	Haematocrit (%)	LK mEq/1 RBC
		$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$
AB	10	72,50±3,54	31,50±0,79	12	39,72±3,56	34,73±1,28	17	97,30±4,35	33,40±1,23	4	35,78±3,57	33,34±1,56
AC	18	73,15±2,15	32,01±0,69	10	37,94±4,59	35,90±1,09	15	100,08±4,52	33,10±1,12	4	34,85±2,01	33,25±1,57
AD	11	75,14±2,75	33,46±1,17	8	36,57±3,94	35,91±1,05	11	108,58±4,98	33,76±1,30	4	40,55±2,71	35,01±1,34
BB	13	76,33±4,96	33,39±1,42	7	30,80±2,46	31,75±1,44	15	106,11±2,58	32,93±1,28	5	34,75±3,65	33,50±1,51
BC	64	77,83±2,51†	35,45±0,43	22	36,26±2,66	35,45±0,74	70	106,34±1,80	34,06±0,36	16	41,36±2,72	34,99±1,02
BD	17	73,19±3,24	33,65±0,74	12	36,08±2,38	36,47±1,08	17	107,41±4,34	33,98±0,75	10	37,17±3,62	35,55±1,36
CC	78	73,50±1,42	33,98±0,40	39	38,83±1,85	34,26±0,50	109	104,59±1,50	33,94±0,33	12	45,53±3,39	35,23±0,99
CD	12	74,48±2,07	32,78±0,59	10	41,86±2,78	35,61±1,47	17	101,65±3,54	34,06±0,86	8	41,80±2,66	33,01±1,02
CE	7	74,01±3,02	32,55±2,75	6	40,19±2,01	35,01±1,24	8	117,68±2,05†	33,63±0,78	4	45,98±2,35	35,51±1,25
DD	10	73,10±3,57	35,73±1,57	8	38,68±2,49	35,08±1,78	10	103,97±2,81	34,35±1,36	8	37,03±2,42	33,63±1,38

† significant at 5 % level.

Table 49. Glutathione and potassium concentrations and haematocrit values of lambs of different transferrin and glutathione and potassium types.

Lamb Tf type	No. of lambs	GSH^H mg/100 ml RBC	Haematocrit (%)	No. of lambs	GSH^h mg/100 ml RBC	Haematocrit (%)	No. of lambs	HK mEq/1 RBC	Haematocrit (%)	No. of lambs	LK mEq/1 RBC	Haematocrit (%)
		$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$		$\bar{x} \pm SE$	$\bar{x} \pm SE$
AB	15	83,76±3,45†	30,36±1,43	10	44,60±2,91	34,75±1,33	15	124,68±3,70†	29,26±0,83	10	33,30±3,71	36,13±1,59
AC	22	82,07±2,45	32,08±0,77	22	43,36±2,49	33,46±0,73	26	112,56±3,09	32,22±0,61	14	42,91±2,76†	34,20±0,99
AD	14	73,51±3,42	33,90±0,59	10	44,28±1,69	31,26±1,10	15	109,68±3,46	32,48±0,99	10	42,75±2,74	33,29±0,72
BB	12	75,88±4,21	30,11±1,66	11	37,90±2,61	33,54±0,89	12	111,06±4,57	32,56±1,01	10	40,27±2,34	30,40±1,96
BC	27	76,70±3,46	31,64±0,49	63	38,02±1,48	33,72±0,37	54	110,70±2,53	32,60±0,38	36	37,11±1,40	33,83±0,52
BD	10	76,53±3,37	29,44±0,74	16	39,72±2,20	32,38±0,78	18	121,77±2,81	30,82±0,82	10	36,74±2,69	32,36±0,90
CC	36	73,47±2,50	32,43±0,44	52	30,70±2,03	33,64±0,53	85	112,33±1,64	33,18±0,36	8	42,07±1,59	32,17±1,09
CD	10	74,35±2,57	31,22±0,56	11	38,48±2,56	34,15±0,91	11	105,37±2,09	33,98±0,89	7	41,09±1,52	32,14±0,75
CE	11	67,76±3,78	32,00±1,13	12	33,41±2,34	31,75±0,46	12	113,73±3,58	31,83±0,81	8	42,37±2,37	32,01±1,01

† significant at 5 % level.

Table 50. Erythrocyte glutathione levels in Finnsheep of different potassium types.

Ewe K^+ type	No. of ewes	GSH^H mg/100 ml RBC $\bar{x} \pm SE$	No. of ewes	GSH^h mg/100 ml RBC $\bar{x} \pm SE$	Lamb K^+ type	No. of lambs	GSH^H mg/100 ml RBC $\bar{x} \pm SE$	No. of lambs	GSH^h mg/100 ml RBC $\bar{x} \pm SE$
HK	188	75,45±1,18†	84	38,75±1,39	HK	146	75,26±1,29†	179	35,26±1,06
LK	39	73,14±2,06	26	33,23±3,21	LK	34	72,99±2,78	59	39,23±1,79

† significant at 5 % level.

Table 51. Erythrocyte potassium levels in Finnsheep of different glutathione types.

Ewe GSH type	No. of ewes	HK mEq/1 RBC $\bar{x} \pm SE$	No. of ewes	LK mEq/1 RBC $\bar{x} \pm SE$	Lamb GSH type	No. of lambs	HK mEq/1 RBC $\bar{x} \pm SE$	No. of lambs	LK mEq/1 RBC $\bar{x} \pm SE$
GSH^H	188	108,58±1,03††	31	39,49±1,12	GSH^H	146	112,66±1,18†	34	43,77±1,71
GSH^h	84	94,48±1,50	26	43,73±3,87	GSH^h	179	106,49±1,24	59	37,35±1,40

† significant at 5 % level.
†† significant at 1 % level.

Table 47 gives the means of GSH and K^+ concentrations in lambs classified by haemoglobin types. The levels of glutathione and potassium (high and low) were higher ($P < 0,05$) in haemoglobin AA lambs than in lambs of other types, whilst AB heterozygotes had higher haematocrit values than AA and BB homozygotes lambs, though not significantly so. As regards the relationships between the GSH and K^+ concentrations and transferrin types, ewes with BC transferrin type had more ($P < 0,05$) GSH in their blood than the other types (67,20 mg/100 ml vs 61,03 mg/100 ml red cells), whereas ewes of CE type had the highest ($P < 0,01$) concentration of K^+. As regards lamb transferrin types and their relation to GSH and K^+ concentrations, the following can be noted from Table 49: AB types had the highest ($P < 0,05$) value of GSH and of K^+ within the HK in their blood, whereas AC transferrin types had the highest concentration of K^+ within the LK level.

3.2.5.2. Erythrocyte glutathione level in relation to blood potassium types in Finnsheep

The mean erythrocyte GSH concentrations of both high and low GSH type sheep in relation to the blood potassium types of the animals are presented in Table 50. It is observed that in the ewes examined, the mean erythrocyte GSH concentration in the HK—GSH-high type ewes was higher than in the LK—GSH-high type ewes. This difference was statistically significant ($P < 0,05$). Similar results were obtained when GSH-low ewes were examined. When the lambs were examined, the mean erythrocyte GSH concentration in the HK—GSH-high type lambs was higher than in the LK—GSH-high type lambs. The mean erythrocyte GSH concentration in the LK—GSH-low type was higher than in the HK—GSH-high type lambs.

3.2.5.3. Potassium concentration in relation to blood glutathione type

The mean potassium concentrations of both high and low K^+ type sheep in relation to blood glutathione types of the animals are included in Table 51. It was found that GSH^h—HK type ewes and lambs had significantly ($P < 0,01$) lower mean red blood cell potassium values than had GSH^H—HK type ewes, whereas GSH^h—LK type ewes had higher mean red blood cell potassium values than had GSH^H—LK type ewes. This was not observed in lambs.

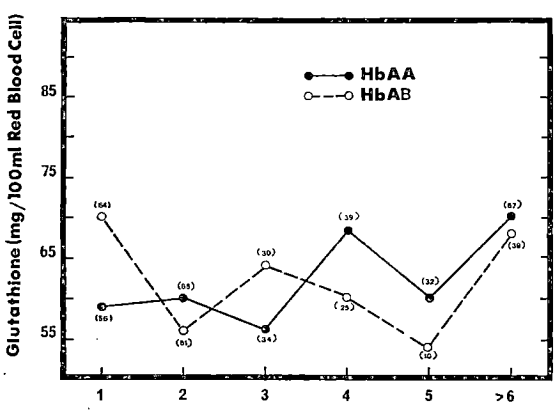


Fig. 22. Mean erythrocyte GSH levels within haemoglobin types and age in Finnsheep, number of animals in parenthesis.

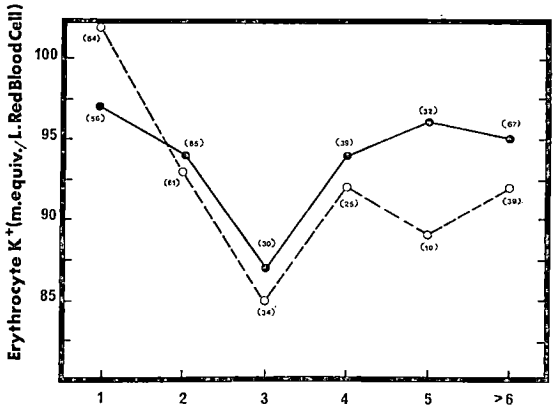


Fig. 23. Mean erythrocyte K^+ levels within haemoglobin types and age in Finnsheep, number of animals in parenthesis.

3.2.5.4. Effect of age and haemoglobin type on blood glutathione and potassium levels

Mean glutathione and potassium concentrations with standard errors at six ages were estimated, and the changes in mean GSH and K^+ with age are shown in Figures 22 and 23. Age of ewe did not have a simple relationship with the mean GSH of the animals, but there was a tendency for GSH level to decline until the animal was three years old, to rise again at the age of 4 years, then drop again in 5-year-old animals, then rise in the 6-year-old animals. The potassium concentration declined rapidly from one year to three years (99,15 mEq/l RBC—87,91 mEq/l RBC), then there was a slight increase, thereafter a decline in 6 year old sheep.

3.3. Discussion

3.3.1. Haemoglobins

It is evident from the results of the present study that the three regions under investigation, namely southern, eastern and northern Finland, all differ in gene frequencies of the haemoglobin types of Finnsheep. Haemoglobin A predominates in all the three regions, the southern and eastern Finland sheep being identical and having the highest gene frequency of Hb^A (0,813). The gene frequency of Hb^B was highest in northern Finland (0,365).

Evans et al. (1958 a) reported the results of a survey of the distribution of haemoglobin types in 33 breeds of sheep in Britain. Among the animals sampled, there were 26 Finnsheep, and no Hb B was observed in them. The results of the present study were significantly different from the results obtained by Evans et al. concerning the frequency of Hb^B (0,365 vs 0,000). There are two possible explanations for this variation: (i) a comparatively large number of animals (1650) were examined in the present survey as compared to the small flock (26) investigated by Evans et al.; (ii) the animals examined by Evans et al. were mainly from southern Finland, where the frequency of Hb^B is relatively low.

According to Evans et al. (1957), sheep in northern Britain and northern Europe tend to be of Hb A type, whereas those in southern Britain, North Africa and the Middle East are of Hb B type. Huisman et al. (1958) found differences in the oxygene dissociation curves of the two sheep haemoglobins, the A type having the greater affinity. These results have been explained by the theory of selective advantages. The B type should not be able to

compete successfully at higher altitudes. The present study shows that the frequency of Hb^B gene in Finnsheep is low in both the southern and eastern regions even though those sheep lived at low altitudes and different latitudes. On the other hand, high frequency of the Hb^B allele was found in northern sheep living at rather high altitudes, at latitudes different from those of the other parts of Finland, and in cold weather. Such a change may have been the cause of the drift in the gene frequency of haemoglobin type A, or may have been due to some other factors, such as origin, artificial selection and environment, to be taken into consideration when this problem is being discussed in detail. It appears, therefore, that if there is any association between haemoglobin types of sheep and geographical location at all, it is less significant than its association with either altitude or temperature alone, or with a combination of both.

The family data in this study bear out the theory of inheritance well. No offspring has a haemoglobin type that diverges from that expected from the haemoglobin types of its parents. A discussion as to whether the departures in the southern flock samples are due to selective differences between genotypes or are an example of the departures from the Hardy-Weinberg expectations, which can occur in domestic animal populations of small effective population size, even when selection is absent (ROBERTSON, 1965), will not be entered into here. Suffice it to say that it is not possible to decide whether either one is, or both are correct solely on the basis of the information available on these flocks.

The data on reproductive performance in the present study show that there are considerable differences in favour of Hb A and possibly some superiority of heterozygotes (especially rams). If animals with haemoglobin A have a marginal superiority over those without, this is in line with the reported superiority of haemoglobin A as a carrier of oxygen, over haemoglobin B (HUISMAN et al., 1958; DAWSON and EVANS, 1962; WATSON et al., 1963). Subsequently OBST and EVANS (1970) suggested that Hb A sheep are physiologically better adapted to harsh, cold environments than Hb B types and therefore have a better reproductive performance under these conditions. Our results seem to support the previously mentioned findings.

As regards the survival data in the present study, there is an advantage of Hb B which is quite big and obvious at some stages of life. On the other hand, the abnormal segregation ratios usually indicate that Hb A has some advantage, but not in all cases. How and when these discrepancies are established is not clear, and one can merely make hypotheses. The fact that there are small differences in fertility among the parental mating types probably indicates that there are some differences in embryonic loss among the offspring genotypes. Differential loss from birth to weaning possibly plays a role in Hb A type, whereas this loss does not appear in differences in mortality from birth to weaning among the offspring of the different parental mating types. If we do not make any distinction between the loss of genotypes of the offspring at birth and that during the period from birth to weaning, and if we assume normal segregation at birth, then this loss is unlikely to be real and implies that differences may be established earlier than at birth. One possibility is that there is differential production of A and B gametes among the parents. It is also possible that there is some differential loss of zygotes from the time of fertilization until implantation if we accept that the number of eggs fertilised is higher than the number of offspring born. The fact that the observed segregation ratios seem to vary considerably from one region to another shows that other factors — possibly relating to the environment — may be involved. The relationship observed between haemoglobin type and lamb mortality supports the postulate presented by EVANS and TURNER (1965); ARORA et al. (1971); and LASSIERA et al. (1976) that haemoglobin A type sheep rear fewer lambs than haemoglobin AB or B type sheep.

The apparent superiority of AA ewes and AB rams in the different production characters, i.e. in the weights of the lambs, may also be considered as evidence of an advantage in homozygotes in ewes and an advantage in heterozygotes in rams. One more outcome in this study which may be of relevance is the discovery of the potential of haemoglobin A type sheep to produce heavier fleeces. The superiority of Hb A type sheep in this respect had been indicated earlier by the observations of WATSON and KHATTAB (1964) and KALLA and GHOSH (1975) in British and Indian sheep.

Production characters of certain sheep breeds are greatly influenced by the factors associated with the harsh conditions in which the sheep live. Some of these are purely environmental, due to lack of food, and exposure to weather. However, these may be modified by factors which are not entirely free of genotypic effects, such as mothering ability, reflected in the early gain of lambs, the protective value of the fleece and grazing habits which are apparently non-random (HUNTER and DAVIES, 1963). For these reasons, a strong relationship between single loci, governing biochemical individuality and production characters, is hardly to be expected. It should be remembered, however, that all the sheep under study have been subjected to intensive selection, and that the genes affecting production traits may, to a certain extent, be expected to be approaching fixation.

3.3.2. Transferrins

There is only one report with information on transferrin phenotypes in Finnsheep, namely that of RASMUSEN and TUCKER (1973). The frequencies of the transferrin alleles found in the Finnsheep of the present study show no important divergence from those found in Finnsheep from England. The dissimilarity in gene frequency of the sheep in the eastern region from the two other regions is of interest. This deviation may be due simply to random genetic drift, or to the differences in environment. Results such as this could have been predicted on the basis of the general theory of the maintenance of variability in a small closed population (e.g. KIMURA, 1955; ROBERTSON, 1962). Obviously a larger population size is needed to avoid genetic drift, particularly at loci with multiple alleles. The Tf^C gene seems to be the most frequent in Finnsheep in all three regions. Tf^A and Tf^E were present at very low frequencies. When the distribution of transferrin phenotypes is also given, CC appears to be in excess of expectation, (KHATTAB et al. (1964) got the same results), suggesting that the polymorphisms are not in equilibrium in many cases. Deviations from the HARDY-WEINBERG equilibrium may be due to a variety of causes (SMITH, 1970) and data from specific matings may be more useful to evaluate selective forces. When the method of incomplete family data (COOPER, 1966) is used to study matings involvning heterozygous rams, there is a highly significant excess of heterozygous offspring. COOPER (1967) observed an excess of heterozygotes in offspring of two rams — one AC and the other AD — which he suggested might be due to inbreeding. The population under study suggests general advantage of heterozygotes when mating involves heterozygous sires. It seems possible that differences in fitness of transferrin types (RASMUSEN and TUCKER, 1973) are most apparent in populations under stress. Perhaps in some cases homozygotes, and in other cases, heterozygotes, have an advantage, according to environment.

It is clearly evident from the results of the present study on reproductive performance that transferrin types of dam and sire influence the number of lambs born and weaned. In this case it is possible to interpret the results obtained in such a way that TfAD of dam and TfBB of sire appear to be at an advantage, compared to other types. However, it is particularly interesting that the results for the transferrin types in the present study do not bear out the findings of RASMUSEN and TUCKER (1973) very well, in which the possession of the allele Tf^D was associated with low fertility in Finnsheep. The fact that there is an association between reproductive performance and transferrin types in

sheep led RASMUSEN and TUCKER (1973) to the conclusion that the transferrin type of sire, dam and offspring somehow clearly influences reproductive performance, but it also seems certain that the effects are not easily measurable. Until recently, the physiological basis of the effects remained obscure. Recently, WELL (1965) showed that the major antigene of seminal spermatozoa in humans and rabbits is derived from the seminal plasma. ROBERTS and BOETTCHER (1969) showed that the antibody against human sperm-coating antigene (SCA) reacts with an iron-binding protein. QUINLIVAN (1968) identified transferrin in human seminal plasma, and MASSON et al. (1968) found another iron-binding protein in the female genital tract, namely lactoferrin. Boettcher, as reported by ASHTON and DENNIS (1971), found that SCA has a mobility identical with transferrin in starch gel but differing from lactoferrin. SCA and lactoferrin both react in immunodiffusion with anti-SCA but transferrin does not. Boettcher suggested that the seminal iron-binding protein, scaferrin, is genetically related to transferrin, that it has some physiological action, and that it is responsible for the observed associations between transferrins and reproductive performance.

A significant effect was obtained for the parameter considered, namely mortality. Tf BD of dam and TF AC of sire appeared to be at a disadvantage compared to other types. The high mortality rates occurring with these genotypes were mainly due to stillbirths and deaths within the first 14 days after birth. The causes of embryonic death in cattle are often discussed but still unknown. It has been suggested that antigen-antibody reactions are responsible for some of the embryonic deaths (KIDDY et al., 1959). In man there is a superstition that early losses of embryos may occur as a result of incompatibility in the ABO blood group system (SHEPPARD, 1959). The possibility that the chance of survival of the bovine embryo is influenced by the transferrin type of the sire and the dam, as suggested by ASHTON (1959 a), has not been excluded. If transferrins do play a role in embryonic survival — and present data suggest that they may — it is possible to assess their function in pregnancy from properties already discovered by other workers. During gestation, the concentration of transferrin in plasma is normally increased. From TURNBULL's and GIBLETT's (1960) work, it does not appear that human transferrins differ in their iron-binding capacity, but there is a possibility that they differ in the ease with which they transfer it to the tissues, thus endowing some genotypes with an advantage which others lack.

As regards the associations between transferrin types and production characters, it should be noted that the results of body and wool weight show little difference in favour of TfAD, whereas the data on lamb weight at different ages show a strong association between transferrin types and lamb gain. The results are consistent with those of Nix et al. (1968), ARORA and ACHARYA (1972) and RAHMAN and KONUK (1977), who reported that the transferrin type has an effect on weight-gain in British, Indian and Turkish sheep respectively.

There are, no doubt, distinct physiological differences between these types which are likely to give an advantage to one type over the other in adaptation to local conditions, but human interference to meet their requirements for mutton or wool or both largely determines the proportion of these types in any given environment.

3.3.3. Potassium

It is evident that HK animals are predominant in the Finnsheep breed, ranging from about 75 % in the east to 87 % in the south. The findings in the present investigation agree with those reported by EVANS and PHILLIPSON (1957) and TUCKER and KILGOUR (1970). These workers showed that HK animals were more common in Finnsheep.

Erythrocyte potassium concentrations in HK type animals revealed that not any of the animals in the two regions appear to fit into any of

KERR's groups (1937). The concentrations of the electrolyte in the erythrocytes of the Finnsheep ranged from 94,48 to 112,67 mEq/l. The mean erythrocyte potassium concentration (K^+) in all these sheep was higher than that which is normally found in British and Indian breeds. This may be characteristic of Finnsheep because it has also been found by other workers (HALLMAN and KARVONEN, 1949). However, the work of BLUNT and EVANS (1963), associating high erythrocyte K^+ with anaemia, may be relevant. It wound be interesting to know whether the high K^+ in a flock of Finnsheep could be lowered by effective anthelmintic chemotherapy. If the potassium remains high in worm-free animals, a blood parasite such as *Eperythrozoon ovis* could be suspected. If it remains high when all precautions against anaemia have been taken, it would be interesting to know why erythrocytes of HK Finnsheep concentrate potassium to a greater extent than most other breeds in the world. There is considerable amount of basic information available on geographical differences in the gene frequencies for potassium types in sheep, but the ecological significance of these findings still largely remains a mystery. Deduction made on the basis of the data collected in one particular climatic zone cannot usually be applied to another zone. There is certainly no reason to suppose that the physiological explanations put forward have general validity. The preponderance of HK animals in Finland may be a reflection of the inherently higher resistance of these animals against bacterial infections (the HK animals have a significantly higher white blood cell count than the LK animals, TANEJA et al., (1966). The second possibility put forward by EVANS and PHILLIPSON (1957), is that HK sheep tolerate a cold, hard climate.

The results of genetic control of K^+ types in Finnsheep suggest that K^L is dominant over K^H and that the blood potassium type is primarily dependent on the segregation of one major gene pair, thus supporting the view of EVANS and KING (1955). It appears that probably the erythrocytic potassium concentration is inherited like other quantitative traits, and is polygenic in nature. The possible explanation of the variability in the LK phenotype could be an incomplete dominance of the LK major gene, heterozygotes having a higher K^+ value than homozygotes, as suggested by EVANS et al. (1956), who recorded a difference between known heterozygotes and a group including both hetero- and homozygotes. Environmental influences may of course provide variability.

There has been an indication (TURNER and KOCH, 1961) that the actual level of potassium ion concentration in the red blood cells for LK sheep may be associated with lamb production. Present evidence suggests that the red blood cell potassium types give an advantage in the number of lambs born in Finnsheep. The LK type sheep appear to have some superiority in number of lambs born over the HK type sheep. It is also interesting to note that the actual level of potassium ion concentration in the red blood cells for HK sheep is associated with the mortality of lamb. EVANS and MOUNIB (1957) suggested that the balance between sodium and potassium might have some bearing on survival in different environments.

Regarding the association between blood potassium types and production characters, the data revealed possible relationships between K^+ types with respect to any of the metrical characters examined. LK type sheep appear to have some superiority in ewe wool and body weight over the other type (HK), whereas HK sheep have been found to have marginally better birth weight and neonatal growth than LK sheep. This bears out similar observation made by WATSON and KHATTAB (1964) and TANEJA and GHOSH (1967), who reported that LK animals tended to have higher wool and body weights than HK animals. Once again, it should be remembered, however, than the majority of production characters are determined by a large number of genes and are influenced by the environment and by many aspects of the animal physiology, and so a strong relationship between the blood potassium types and production characters is hardly to be expected.

3.3.4. Glutathione

An interesting aspect of this study is the finding that the high-GSH type (GSH^H) predominates in southern sheep, whereas the frequency of the two alleles present in eastern sheep, GSH^H and GSH^h, was found to be very near a 50:50 distribution. It appears that considerable differences do exist in this respect, but it is as yet too early to attempt an explanation for the differences in distribution. Nevertheless, some environmental, nutritional or breeding differences may influence GSH concentration. Earlier, TUCKER and KILGOUR (1970) had reported a preponderance of GSH^H type in the breed of Finnsheep examined by them in England. Of the six breeds examined by the authors, only the Finnish Landrace had an appreciable number of GSH^h animals.

The data presented in this thesis may suggest that Finnsheep erythrocyte GSH concentration is regulated by a pair of autosomal alleles, the allele for high GSH concentration being dominant and that this main gene effect is modified by other heritable factors. In this thesis, there is a suggestion that the dominance of the GSH^H gene might not be complete. If the GSH^H progeny from Table 36 were divided into two groups, in one of which all are heterozygotes (the GSH^H offspring from $GSH^h \times GSH^H$ matings) and in the other of which there are presumably both homozygotes and heterozygotes (the GSH^H offspring of $GSH^H \times GSH^H$ matings), the known heterozygote group would have a significantly ($P < 0{,}01$) lower mean erythrocyte GSH level than the mixed homozygote/heterozygote group (Table 37). The values obtained were not related to the mean value of the GSH^H parents. However, if the dominance were incomplete, one would expect the mean value for phenotypically GSH^h animals to have a lower standard error than that for phenotypically GSH^H animals. This has not been observed in the present study (Table 38). However, it should be noted that the number of low-GSH type animals arising from the high-GSH mating should exceed the number expected if a HARDY—WEINBERG equilibrium exists; this in turn suggests a deficiency of the homozygous high-GSH type in the parental population. The results presented here support the hypothesis that the red blood GSH deficiencies found in the Finnsheep breed are under genetic control and that, in effect, the gene for low GSH is recessive and the one for high GSH is dominant (TUCKER and KILGOUR, 1970 and 1972).

So far, no work has been reported on the association between the glutathione types and reproductive performance in sheep. In the present study, the number of lambs born was estimated for Finnsheep differing in red blood cell glutathione; ewes with a high-GSH type maintained a higher number of lambs than those with low-GSH type.

It is also interesting to note that high mortality in lambs of Finnsheep is strongly associated with low-GSH type. The high mortality rates occurring in GSH^h types were mainly due to stillbirths and deaths within the first 14 days of life. In this respect it is of particular interest that the results for the glutathione types of the present thesis do confirm the findings of TUCKER et al. (1976), who reported that mortality of »double-low» GSH lambs (in their plan of backcross experiments, Finn × Merino × Finn with the aim of producing »double-low» GSH genotypes) was significantly higher from that of high-GSH animals. Erythrocyte GSH levels have been shown to be associated with milk yield and body size in cattle (KIDWELL et al., 1955; SLEPKOVE, 1961; and BORSKENKO, 1961) and fleece weight in sheep (SALTYKOVS, 1956). It appears from the present results that sheep with high-GSH type have greater body weight and yield more wool than low-GSH type sheep. AGAR et al. (1972) reported a positive correlation between both body and wool weight and high-GSH type in Merino sheep.

One more outcome of this study of possible relevance is the potential of high-GSH type sheep for producing heavier lambs at 3 days and 8 weeks of age. The relative association between blood glutathione and growth rate in

this respect has been studied in Nilagiri sheep in India (KANDASAMY et al., 1976).

It appears that erythrocyte GSH types are genetically controlled, and that the GSH concentration within these types is highly heritable (BOARD et al., 1974). It is therefore possible that further investigation on the relationships of GSH types and economic traits might provide information of interest to livestock breeders.

3.3.5. The association between the various blood polymorphic characters

In common with EVANS et al. (1958), MOUNIB and EVANS (1959), DAWASON and EVANS (1962) and KHATTAB et al. (1964), the results of the present study show evidence of an association between the polymorphic characters. Sheep possessing the Hb B gene had higher GSH levels and lower haematocrit levels than sheep with Hb A, whilst sheep with the Hb A gene had higher K^+ and haematocrit levels than those with Hb B. One more outcome is that sheep possessing the Tf BC genotype proved to have higher GSH levels in their blood, and those of Tf CE higher K^+ levels.

Differences in erythrocyte glutathione and potassium concentration between animals of different haemoglobin- and transferrin- types have been noted before. However, these differences have not been explained. KHATTAB et al. (1964) suggested that the various known haemoglobin types are sufficient to account for the variations observed in whole blood potassium.

The results presented is this thesis support the observations of TUCKER and KILGOUR (1970), AGAR et al. (1972), and HOPKINS et al. (1975), that GSH^h animals have a lower mean erythrocyte potassium concentration than GSH^H animals in both HK and LK groups. However, our results were different from the findings mentioned earlier concerning the LK group of ewes; it was also found that the mean erythrocyte GSH concentration in HK—GSH-high type animals was higher than in LK—GSH-high types. However, KALLA et al. (1972), found the reverse in the Indian sheep. It is possible that the association between erythrocyte levels varies from breed to breed.

A negative correlation between erythrocyte GSH concentration and haematocrit value ($r = -0{,}186$, $P < 0{,}05$) was also found. A similar relationship was found between the erythrocyte K^+ concentration and the haematocrit value ($r = -0{,}229$, $P < 0{,}01$). A negative relationship between the haematocrit value and the erythrocyte GSH concentration has been reported in man (CERNOCH and MALINSKA, 1966). WIDDAS (1954) showed a decrease with age in the K^+ concentration of foetal lambs from Welsh Mountain sheep. WRIGHT et al. (1958) estimated potassium concentrations in the blood of lambs over the period 12 to 60 days after birth, and concluded that with advancing age there is a decrease in the potassium concentration. Similar results were obtained by KOCH and TURNER (1961). The results, presented here suggest a decrease with age in K^+ concentration. It is also noted that the concentration of potassium in HK type lambs is higher than in HK type of ewes; the reverse was found to be true in LK type.

An increase in erythrocyte GSH with age has been reported in man (BERTOLINI et al., 1962; GOLDSCHMIDT, 1970), while ZINKHAM (1959) found no significant differences in GSH values between newborn babies and adult men. The relationship between erythrocyte GSH and age in ruminants, however, has been the subject of conflicting reports. REID et al. (1948) reported an increase in erythrocyte GSH with age in cattle. KUNKEL (1954) found no difference in GSH values between calves and adult cattle, while GURTLER et al. (1965), PODGORSKI and MAJEWSKI (1969) and MABON (1969) reported higher values in calves than in adults. In sheep KIDWELL et al. (1958) reported no difference between GSH levels of lambs and ewes, while AGAR et al. (1972) found an increase in erythrocyte GSH with age in sheep. The results presented here suggest that erythrocyte low-GSH values are higher in lambs than the low-GSH value in adult ewes.

A deficiency of GSH in the red cells of sheep is unaccompanied by an apparent haemolytic disorder (SMITH and OSBURN, 1967). This study shows sheep having GSH values ranging from less than 5 mg/100 ml RBC to 190 mg/100 ml RBC, these animals being apparently normal with regard to haemoglobin concentration, haematocrit value and erythrocyte level. It is difficult to believe that such great differences in red cell GSH level are not accompanied by other inherent differences of a compensatory nature in the biochemistry of the red cell.

3.3.6. Conclusions

What conclusions can be drawn from the foregoing discussion, and to what extent will an increased knowledge contribute to developments in the applied field? The answer to this question will obviously require combined chemical, biological and genetical approaches. However, in this new field of study it is neither possible nor advisable to come to any firm conclusions as to the relative potential of each of the blood characters available to increase measures of adaptation and productivity. Nevertheless, there is no doubt that the red blood cell characters are genetically controlled. This kind of evidence continues to suggest that polymorphism at these loci in fact has a selective advantage. However, both the genetic control and biochemical structure have opened a field of speculation as to possible relations between blood characters and other genetically determined traits, in which the breeders of the animals are interested.

It is also attractive to believe that variant forms of these characters confer some advantage under appropriate conditions associated with climate, nutrition, or — more likely — disease, although the ecological significance of these findings still largely remains obscure. Obviously, from the point of view of biological genetics, the evolution of Finnsheep must remain largely speculative at the moment, and more research is necessary if speculation is to be replaced by fact.

There has been some convincing evidence that knowledge of blood biochemical characters of sheep might be used in breeding to improve stock; let us hope that this knowledge will be revealed in more detail in the future. The fact remains, however, that polymorphism of biochemical variants is common in sheep and that inbreeding apparently does not lead to the expected increase in degrees of fixation at many of these loci (LERNER & DONALD, 1966). It is difficult to explain how it is that these polymorphisms are maintained and what the circumstances are that maintain them, for it could be argued that any detrimental factors would have disappeared by now as a result of intensive selection. Estrus, fertilization and gestation comprise a complex sequence. They are subject to the action and interaction of an even more complex set of factors — environmental, psychological, neural, chemical and hormonal actions and interactions — which prepare and maintain or fail to maintain pregnancy and embryonic and foetal development, and it follows therefore that most inherited characters of economic importance are the net result of the activity of genes at a large number of loci.

It is interesting, and should be instructive, to consider the opinions of several workers as to the future potential of the present methods which are available to improve animal production. JOHANSSON and RENDEL (1968) concluded that a very slight positive effect on the fertility and vigour of the animals by a certain gene in a special environment could, by natural selection, lead to gene frequency differences. LERNER and DONALD (1966) state that principles derived from basic research must underlie development and they quote STORER (1963) who suggests that »we must expect to find that basic research will become the tail rather than the dog in coming years. Unless knowledgeable efforts are made to protect it, we may find it being wagged right off the dog without being aware of it... When applied research comes to dominate science, it will come under the guise of basic research». However, as we

learn more about the biochemical genetics, both of individual cells and of the whole organism, we can begin to hope that in the future it may be possible to introduce genetic considerations into schemes for providing the correct nutritional requirements for farm animals or the correct animals for a particular environment.

3.4. Summary

1. A total of 1650 blood samples from the Finnsheep breed was collected and analysed for haemoglobin types. All three haemoglobin types — A, B and AB — were found to be present in the animals examined. Haemoglobin A animals predominated in Finnsheep. The frequencies of alleles Hb^A and Hb^B in sheep averaged 0,748 and 0,252 respectively. Haemoglobin types in sheep are genetically controlled by a single pair of allelic genes with co-dominance and are inherited in a simple Mendelian manner.

Haemoglobin types were examined in relation to reproductive performance, lamb weight at different ages and mortality of lambs. Haemoglobins A and AB appeared to have an advantage in fertility over haemoglobin B. As to the fecundity of rams with different haemoglobin types there was a similar tendency as for ewes.

The number of lambs weaned produced by different types of ewes differed significantly. Haemoglobin B produced a large number of weaned lambs.

Haemoglobin types of ewes had only a small influence on body and wool weight. Ewes of haemoglobin type A had greater body and wool weights than ewes of blood type AB and B. Analysis of the association between haemoglobin types and lamb weight at birth, 3-days, 3, 6, and 8 weeks and 4 and 5 months in Finnsheep, showed that ewes with Hb A type had a significant influence on 3-day, 6-week and weaning weights only. Lambs of haemoglobin type B had higher 5-month weights than lambs of haemoglobin type A and AB. The possible significance of these findings is discussed.

2. The transferrins of sheep in three regions were studied by means of starch-gel electrophoresis. Five transferrin types, Tf^A, Tf^B, Tf^C, Tf^D and Tf^E, were observed in Finnsheep. Gene frequencies were calculated for each region. Considerable variation was found in frequency of the transferrin alleles between the regions. The frequencies of the transferrin alleles found were $Tf^A = 0{,}056$, $Tf^B = 0{,}226$, $Tf^C = 0{,}620$, $Tf^D = 0{,}075$ and $Tf^E = 0{,}023$.

Progeny data were generally in agreement with the five-allele theory of inheritance. A comparison of observed phenotype frequencies with those expected under random mating showed that there existed a marked disturbance in segregation, with homozygous Tf CC animals in excess and a marked shortage of heterozygous Tf CE animals.

The possible relation of transferrin type to reproductive performance, lamb weights at different ages and ewe body and wool weights was studied. Tf AD of dam and Tf BB of sire appeared to have an advantage in the number of lambs born over other mating types, whereas Tf BD of dam and Tf AC of sire seemed to have a significant disadvantage in the mortality of their lambs. The effect of tranferrin types on ewe body and wool weight showed that the Tf AD appeared to have a slight advantage over the other types.

The effect of transferrin type on some preweaning performance traits was found to be significant for 3-day, 3, 6 and 8 week weights and also weaning weight. The characteristics of the transferrin types and the possibility of selection on the basis of transferrin types for improved production characters were discussed.

3. Blood samples of Finnsheep from two regions in Finland were analysed for concentration of potassium in the whole blood. On this basis, sheep were classified into high (HK) and low (LK) potassium types. High potassium (HK) type predominated in Finnsheep. The inheritance of potassium concentration in sheep appears to be polygenic in nature. The detectable association of these polymorphic characters

with reproductive performance, lamb weights at different ages, ewe body and wool weight was examined. There was an indication that ewes and rams with LK type have a better reproductive performance, whereas HK type sheep weaned significantly more lambs than did LK type sheep. The potassium types showed small differences in ewe body and wool weights. On the whole, sheep of LK type tended to have greater wool and body weights than sheep of HK type. Blood potassium type of rams and ewes and their lambs had only small influence on birth, preweaning and weaning weights. Sheep of HK type had a slightly better birthweight and neonatal growth than LK sheep.

4. Blood glutathione concentrations were measured in Finnsheep in two regions. On the basis of concentration of glutathione in the whole blood, sheep were classified into high (GSH^H) and low (GSH^h) glutathione types. There are about 61 % GSH^H sheep in the southern region, whereas the frequencies of the two alleles present in the eastern sheep, GSH^H and GSH^h were found to be very near a 50:50 distribution. The genetic control of the level of reduced glutathione in the erythrocytes of pure bred Finnsheep was investigated. The data suggest that the erythrocyte GSH levels are controlled by a single pair of autosomal alleles, the gene for GSH^H being dominant.

The nature of the association between glutathione types and reproduction performance, lamb weight at different ages, ewe body and wool weight and lamb mortality in these sheep was examined. GSH levels were found to be associated with the number of lambs born — GSH^H appeared to have an advantage over GSH^h. An important factor of this investigation was that GSH type was found to be associated with lamb mortality.

Regarding production characters viz. ewe body and wool weights and lamb weights at different ages, mean weights were found to be larger in animals of GSH^H type than in GSH^h type animals.

5. The association between the different polymorphic characters was examined in Finnsheep. Blood glutathione and potassium were found to be associated with haematocritic values, haemoglobin and transferrin types in these sheep. The relationship between age and glutathione and potassium concentration was also investigated. The significance of these findings was discussed.

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SELOSTUS

Suomenlampaan tuotanto- ja lisääntymisominaisuuksien ja veren biokemiallisten, polymorfisten ominaisuuksien välinen fenotyyppinen ja geneettinen yhteys.

Tutkimusta varten kerättiin suomenlampaista — pässeistä, uuhista ja niiden karitsoista — yhteensä 1 650 verinäytettä 19 tarkkailutilalta Pohjois-, Itä- ja Etelä-Suomesta. Kaikista määritettiin hemoglobiini- ja transferriinityypit ja Itä- ja Etelä-Suomen 760 näytteestä määritettiin myöskin glutationi- ja kalipitoisuudet. Hb- ja Tf-tyypit määritettiin tärkkelysgeelielektroforeesilla ja GSH- ja K-pitoisuudet atomiabsorptiospektrofotometrillä.

Tutkittiin emän ja isän verityyppien vaikutusta yhdessä ja erikseen lisääntymisominaisuuksiin — sikiävyys ja karitsakuolleisuus — ja muihin tuotanto-ominaisuuksiin — karitsan paino eri ikävaiheissa (syntymähetki, 3 pv, 3 vk, 6 vk, 8 vk, 4 kk ja 5 kk) ja uuhen elopaino ja villanpaino. Lisäksi tutkittiin karitsan verityypin vaikutusta sen painoon eri ikä-vaiheissa sekä tutkittiin veriominaisuuksien välisiä yhteyksiä. Analyysimenetelmänä käytettiin hierarkkista varianssianalyysia.

Kaikki kolme Hb-tyyppiä — AA, AB ja BB — esiintyi tutkituissa eläimissä. Hb A:n ja Hb B:n alleelifrekvenssit olivat vastaavasti 0,748 ja 0,252. Lampaan Hb-tyypin määrää yksi alleelipari. AA- ja AB-tyyppisille uuhille ja pässeille syntyi enemmän karitsoita kuin BB-tyyppisille. Sen sijaan BB-tyypillä vieroitettujen karitsoiden osuus syntyneistä oli merkitsevästi suurempi kuin AA- ja AB-tyypeillä.

Karitsapainoissa 3 pv:n, 6 vk:n ja 4 kk:n iässä oli uuhilla AA-tyyppi merkitsevästi muita parempi. AA-tyyppiset uuhet olivat myöskin muita painavampia ja tuottivat enemmän villaa. BB-tyyppiset karitsat olivat muita painavampia 5 kk:n iässä.

Viisi transferriiniä — Tf^A, Tf^B, Tf^C, Tf^D ja Tf^E — ja kaikki 15 mahdollista fenotyyppiä esiintyi tutkitussa lammaspopulaatiossa. Alleelifrekvenssit, jotka vaihtelivat suuresti eri alueiden välillä, olivat koko maassa: Tf^A = 0,056, Tf^B = 0,226, Tf^C = 0,620, Tf^D = 0,075 ja Tf^E = 0,023.

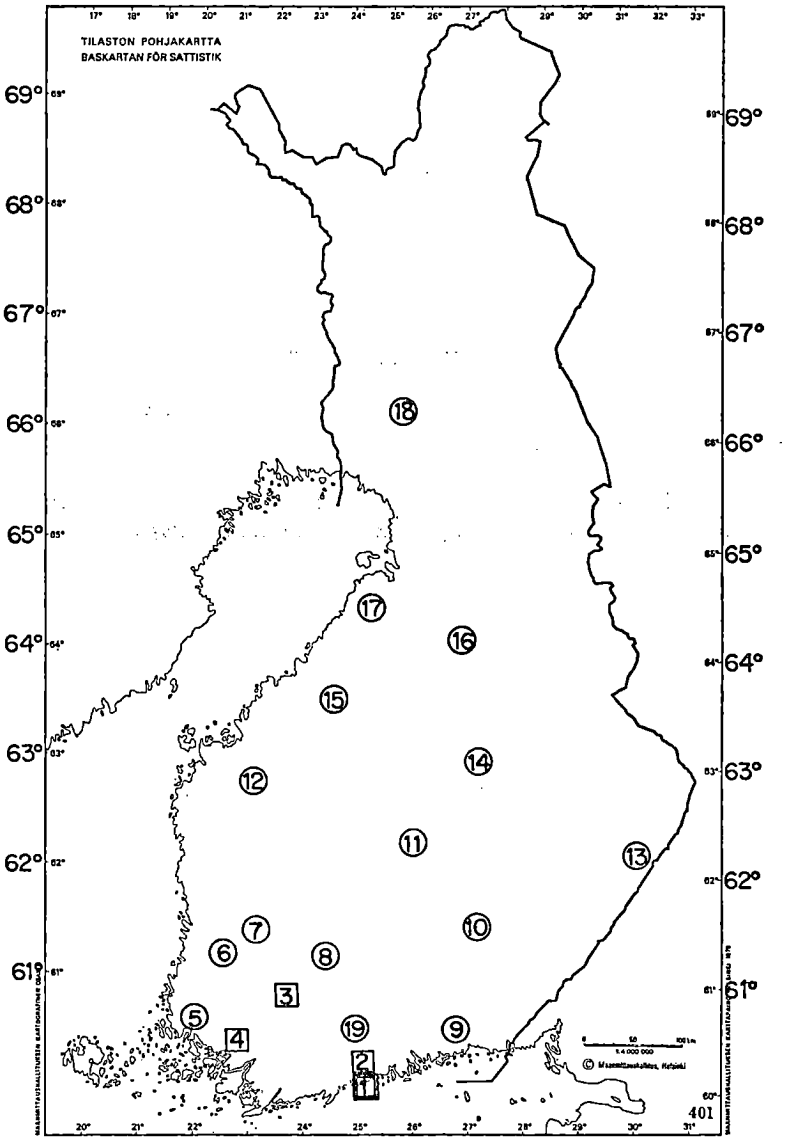
Sekä emän että isän Tf-tyyppi vaikutti syntyneiden karitsoiden lukumäärään. AD-tyyppiset uuhet olivat keskimäärin muita sikiävämpiä. BB-tyyppi pässillä vaikutti positiivisesti karitsalukuun. Karitsapainoihin nähden olivat yleensä BC- ja CC-tyypit parhaat, oli kyse sitten uuhista, pässeistä tai karitsoista.

Veren K-pitoisuuden mukaan lampaat luokiteltiin kahteen ryhmään, HK-tyyppi > 70 mEq/litra punasoluja ja LK-tyyppi ≤ 70 mEq. HK-tyyppi oli tutkitussa suomenlammaspopulaatiossa yleisin.

Syntyneiden karitsoiden lukumäärään nähden LK-tyyppi oli paras sekä uuhilla että pässeillä, mutta vieroitettujen karitsoiden lukumäärään nähden HK-tyyppi oli paras. Yleensä ottaen LK-tyyppiset uuhet olivat painavimmat ja tuottivat eniten villaa. Muissa tuotanto-ominaisuuksia kuvaavissa mitoissa ei ollut suurta eroa eri K-tyyppien välillä, joskin HK-tyyppi oli hiukan parempi karitsapainoissa.

Veren GSH-pitoisuuden perusteella lampaat luokiteltiin kahteen ryhmään, GSH^H > 55 mg/100 ml punasoluja ja GSH^h ≤ 55 mg. Etelä-Suomen lampaista 61 % oli GSH^H-tyyppiä, muualla oli suurin piirtein yhtä paljon GSH^H- ja GSH^h-tyyppisiä eläimiä. Periytymistulosten perusteella GSH-tason määrää yksi autosomaalinen alleelipari ja GSH^H on dominoiva.

GSH^H-tyyppisillä uuhilla oli enemmän sekä syntyneitä että vieroitettuja karitsoita. GSH^h-tyyppi vaikutti negatiivisesti karitsoiden elinkelpoisuuteen sekä uuhilla että pässeillä. Myös muissa ominaisuuksissa GSH^H-tyyppi oli yleensä edullisin.



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