A PHYSIOLOGICAL APPROACH TO BREEDING FOR ENVIRONMENT

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Summary

The present position with respect to haemoglobin types and potassium types in sheep and their possible association with reproduction and environment are discussed.

I. INTRODUCTION

In 1954, the potassium polymorphism which occurs in sheep red blood cells was noted independently by Widdas (1954) and by Evans (1954). Subsequently, Harris and Warren (1955) published their findings on sheep haemoglobin polymorphism. A short summary of the findings since these early papers is given below.

II. HAEMOGLOBIN POLYMORPHISM IN SHEEP

Evans et ***al.*** (1956) showed that the two major sheep haemoglobins are determined by an allelic pair. Later work reviewed by Agar (1968), confirmed these findings.

Evans and Mounib (1957) and Evans, Harris and Warren (1958a, 1958b) reported that British breeds which had a high gene frequency for haemoglobin A tended to have a high gene frequency for high red blood cell potassium (HK). Hb A and HK tended to be more common in the north and in mountainous areas, and Hb B was the most common in North Africa and the Middle East.

Huisman, Van Vliet and Sebens (1958) reported a difference between the oxygen dissociation curves of the two sheep haemoglobins and suggested that natural selection would favour haemoglobin A at high altitudes. They also postulated an advantage for Hb B at sea level. The difference in oxygen dissociation curves has been confirmed (Dawson and Evans 1962; Naughton ***et al.*** 1963; Sirs 1966). Dawson and Evans (1962) reported that within either haemoglobin type the oxygen dissociation curve of the HK cells is to the left of that of the low potassium (LK) cells.

Numerous papers have since been published reporting gene frequencies for haemoglobin types in different sheep breeds. These have been summarized by Agar (1968). They tend to confirm the original contention of Evans, Harris and Warren (1958a, 1958b) that Hb A appears to be associated with mountainous or-

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relatively cold areas. King et *al.* (1958) attempted to associate production characters with genetic characters in Scottish Blackface ewes. They did not find any significant differences but noted that LK and Hb B type ewes (which in Scottish Blackface are quite rare) may have been associated with a higher birth weight and weaning weight in their lambs. Evans and Blunt (1961) examined two British breeds of sheep on the Southern Tablelands of New South Wales and showed that the gene frequency for Hb B in flocks established over a long period in this environment was higher than for these same breeds in Great Britain — a possible gene/environment interaction.

Watson and Khattab (1964) investigated certain economic characters in Welsh Mountain sheep of different haemoglobin and blood potassium types and found no significant differences between types. However, they mentioned that there was a possibility that fleece weight in Hb A animals was greater and that LK ewes produced slightly heavier lambs.

Ghosh, Eyal and Evans (1965) showed that Awassi sheep in Israel kept for milk production were exclusively Hb B and in the same year Evans and Turner (1965) showed that Hb B Merino ewes at two localities in warm dry areas of eastern Australia had significantly higher lambing and weaning percentages than Hb A ewes. Dooley (1965) working with Merinos in inland New South Wales also showed that Hb B type ewes produced more lambs. Bernoco (1967, 1968) has stated that, in Italy, Langhe ewes carrying the Hb B and LK genes appear to be superior to other gene types both in the number of lambs produced and in the number of lambs weaned. On the other hand, Meyer, Lohse and Gröning (196.7) working in Northern Germany with Blackheaded Mutton sheep have reported that ewes of Hb A or AB type and HK type are more fertile than Hb B - LK ewes.

The different environments in which the research had been undertaken could have influenced the results obtained. There was reasonable evidence however to postulate that Hb B Merinos could be at an advantage in some environments in Australia. A balanced polymorphism based on the effects of environment or other selection pressures could be operating. (Gene frequencies for Hb A in Merino flocks examined by the authors have ranged between 0.18 and 0.61).

As the Merino flocks, which had relatively high gene frequencies for Hb A, tended to be in the colder wetter areas of Australia (a similar situation to northern Europe) the idea evolved that a lamb with the Hb A gene might be at an advantage if it were born during cold bleak weather. Obst (1968) and Obst and Evans (1970) have produced evidence which tends to support the above thesis. They found that, when environmental conditions were unfavourable during the time of lambing, lambs from Hb A ewes survived significantly better than those from Hb B ewes.

A physiological explanation for the balanced polymorphism which has been observed in haemoglobin types in sheep breeds is, therefore, possible.

Hb B should predominate in warm environments because of its apparently better reproductive performance. Eyal (1968) working in Israel with Awassi X Friesian ewes showed a distinct advantage of Hb B ewes over Hb AB ewes with respect to lambing percentages. He also noted that the culling rate for Hb B ewes was approximately half that for Hb AB ewes. Dr. Eyal has sent us some of his more recent unpublished data, which confirm the original findings and also suggest that, in the environment in which he was working, Hb B may also have other production advantages. We understand that sheep being imported into Israel are now haemoglobin typed prior to purchase, so that the Hb B gene pool in their flocks will not be diluted.

The present authors believe that there is good evidence for a relationship between Hb type, reproductive performance and possibly also production, and that this relationship is modified by environmental factors. They also believe that the mobility of sheep within Australia has tended to mitigate against strains being developed for specific environments (cf. Britain). Perhaps strains could be developed for specific areas of this continent. The authors believe that this thesis should now be-tested in the field.

III. RED BLOOD CELL POTASSIUM TYPES IN SHEEP

Three early workers in the field presented data which suggested a red blood cell potassium polymorphism (Abderhalden 1898; Kerr 1937; Hallman and Karvonen 1949).

Widdas (1954) and Evans (1954) demonstrated this polymorphism within breeds and Evans and King (1955) showed that HK and LK are simply inherited, LK being dominant. This has been confirmed (see Agar 1968).

Anatomical and physiological differences between HK and LK erythrocytes have been demonstrated (Mounib and Evans 1959). Higher erythrocyte and leucocyte counts were demonstrated in HK animals in India by Taneja, Fuladi and Abichandani (1966). Tosteson (1963, 1966) showed that S.ATPase activity is about four times greater in HK red blood cells, and Eaton ***et al. (1967)*** observed A.T.P. levels to be 31 per cent greater in HK red blood cells. Rasmussen & Hall (1966a, 1966b) have associated the HK gene with sheep blood group M. Ellory & Tucker (1969) were able to stimulate the potassium active transport system in LK erythrocytes by sensitizing them ***in vitro*** with anti-m serum. Whether within the LK type there is a relationship between the actual $[K_e^+]$ and M antigen activity is not known. In view of the possible relationship between actual $[K_e^+]$ of LK Merino sheep and wool production, mentioned below, a relationship of this nature, if it exists, could have a very real practical significance.

The mean $[K_e^+]$ in Scottish Blackface sheep is approximately 22.0 m-equiv./l. RBC, while that in the Merino is approximately 12.0 m-equiv./1. The evidence given by Evans & Phillipson (1957) that these levels are inherited has been supported by Kidwell ***et al.*** (1959) and Sartore (1961) but not by Darcel, Simpson and Avery (1961) or Kraay, Gaillard and Brouwer (1961). The evidence presented by Evans and Phillipson (1957), however, seem quite conclusive.

In some areas of the world (particularly North Africa, The Middle East and India), the HK type is not necessarily the same as that found in Northern Europe. The peculiar HK type present in these areas has been called δ by Evans (1957) and is now being intensively studied in the Merino breed in Australia by the present authors (Evans, Roberts and Agar 1970).

Apart from the one report by Meyer, Lohse and Gröning (1967) that HK and Hb A were associated with a reproductive advantage in their environment, there has been little evidence to suggest the superiority of either LK or HK type with respect to either production or reproduction. The exception to this statement revolves around the differentiation of HK into three sub-types — β, γ, δ (Evans 1957). The data presented by Ghosh, Eyal and Evans (1965) suggest that flock masters selecting Awassi sheep for high milk production in Israel had unknowingly increased quite markedly the number of 8 type animals in their flock. This observation stimulated research into the possible physiological differences between δ type animals, which seem to be more common in breeds associated with warm dry environments, and the normal European HK type (8 subtype). This research has shown that δ type animals have some erythrocyte characteristics that are unusual in sheep but approach those normally found in camels (Evans, Roberts and Agar 1970). These authors showed that δ type sheep have a very high mean corpuscular haemoglobin concentration (42 per cent compared with the camel 49 per cent and the γ HK sheep 34 per cent) and a median corpuscular fragility which is very low for sheep (also a typical feature of camel cells).

Delta type animals are found in breeds and in areas where Hb B predominates and, as van der Helm, van Vliet & Huisman 1957) have shown that Hb B is more soluble than Hb A, there is the possibility that the combination of a high MCHC (as found in δ animals) with Hb A is disadvantageous.

A flock of HK (δ type) — Hb B Merinos is being developed at present at the Department of Physiology, University of New England.

The gene frequency for LK in Australian Merinos is very high (approximately 0.94). The Spanish Merino from which they are descended also has a high gene frequency for LK. In both areas (Spain and Australia) the Merino tends to be associated with arid and semi-arid environments. Physiological evidence, however, which would enable one to associate LK with desert conditions, is not great but a low [K_e^+] in LK Merinos has recently been shown to be associated with high spinning counts Evans, Burr, Roberts, Moodie, McQuirk and Barlow, unpublished data) and possibly drought survival (D. J. Forrest, personal communication). The fact that the Merino in Spain and in Australia has been bred for a long time for semi-arid environments and for fine wool production could be the reason for its high gene frequency for LK and its unusually low [K_e^+]. In India, those sheep which have been selected for survival rather than fine wool tend to have a low gene frequency for LK.

There is thus evidence that a low actual [K_e^+] within the LK type may be associated with fine wool production and drought survival. There is no real physiological evidence, however, to suggest that either of the two main potassium types [LK or HK (8)] is at an advantage in arid environments. On the other hand extrapolation from laboratory results and some field evidence suggests that HK (δ) may be superior in some environments (possibly including arid environments), and the present authors believe that this type, in the Merino, would re-pay intensive study.

Research in this field since 1954 has demonstrated that the genes for haemoglobin type and potassium type, which have been discussed in this paper, have effects on the physiology of the individual, and that they also appear to be related to reproduction and production, their expression being modified by environment. We believe that the evidence to date suggests that economic exploitation of these genes may be possible and that the sheep industry — through research organisations which have the man power and facilities which a thorough testing would require — should test this thesis at the extensive, but non-commercial level. The biological interactions in this thesis are complex but the research reviewed here suggests that a thorough study of these interactions could lead to economic advantages to the end-user — the grazier.

IV. REFERENCES

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