Note

Haemoglobin type frequencies in the Assaf (Awassi × East Friesian) dairy sheep 20 years after its formation

E. GOOTWINE

Institute of Animal Science, Agricultural Research Organization, Bet Dagan, Israel

Summary

Haemoglobin allele frequencies were examined in 195 ewes and 6 rams belonging to the Assaf cross (Awassi × East Friesian). The frequency of the Hb A allele was 0.14 indicating a decline in Hb A frequency in the Assaf during the last 20 years. Ewes belonging to the AB genotype showed a significant advantage over the BB genotype in both lamb and milk production in the first lactation. It is suggested that the haemoglobin polymorphism in the Assaf is maintained due to an advantage of AB heterozygotes for production and survival.

Key words : sheep, haemoglobin, Assaf breed, milk production, lamb production.

Résumé

Fréquences des types d’hémoglobine dans la race ovine laitière Assaf (Awassi × Frisonne de l’Est) 20 ans après sa création

Les fréquences des allèles hémoglobine ont été étudiées chez 195 brebis et six béliers de la race Assaf (Awassi × Frisonne de l’Est). La fréquence de l’allèle Hb A est de 0,14, indiquant une diminution de la fréquence de cet allèle chez les Assaf au cours des 20 dernières années. Les brebis de génotype AB possèdent une supériorité significative sur celles de génotype BB, tant pour la production d’agneaux que pour la production laitière en première lactation. Il est suggéré que le polymorphisme de l’hémoglobine est maintenu dans la race Assaf grâce à un avantage des hétérozygotes AB pour les caractères de production et de viabilité.

Mots clés : ovin, hémoglobine, race Assaf, production laitière, production d’agneaux.

I. Introduction

Two main electrophoretic types of sheep haemoglobin (Hb), designated A and B, have been described (HARRIS & WARREN, 1955). These types, which were shown to be
determined by two alleles at a single locus (Evans et al., 1956), give rise to three genotypes: AA, AB and BB. Allele frequencies of Hb types vary among breeds of sheep (see review by Agar et al., 1972). Following the observation that flocks in which Hb A is predominant are confined to latitudes above 40°, the theory was advanced that Hb polymorphism may have adaptive significance. The study of Evans & Blunt (1961), showing that movement of a breed away from its place of origin appears to have an effect on the Hb allele frequencies, supports this idea.

Adaptation to the environment is of great importance in determining animal performance. In line with this, the relationship between Hb types and productive and reproductive traits has been examined by a number of authors (Agar et al., 1972; Templeton et al., 1972; Pant & Pandey, 1975; Gootwine & Goot, 1979; Dally et al., 1980).

The allele A frequency in the fat-tail Awassi sheep in Israel is very low — less than 2% (Evans et al., 1958). The prolificacy of the breed is rather low (1.2 lambs/ewe/lambing) and in order to increase lamb production in dairy flocks, crossbreeding between the Awassi and the East Friesian breeds was carried out in the 1960's (Goot, 1966; Eyal et al., 1978), resulting in the formation of the synthetic Assaf breed. At present, most of the dairy ewes in Israel (approximately 8000 head) are of the Assaf breed. The frequency of the Hb A allele in the F1 of the cross was found to be 0.38, a value intermediate between the frequencies in the parental breeds (Reshef, 1965). However, with time, the frequency of allele A was reduced, and reached 0.22 in the F3. In another study (Eyal, 1968), it was found that Assaf ewes belonging to the BB genotype produce more lambs and have a longer life span than ewes with the AB genotype. On the other hand, ewes with the AB genotype were found to produce more milk.

During the last 20 years the Assaf population has been subjected to both artificial (milk and lamb production) and natural selection. The objective of this study was to examine present Hb allele frequencies in the Assaf in relation to their possible adaptive value.

II. Material and methods

The study was conducted in the Newe Ya'ar Assaf dairy flock in which an Hb survey had been carried out approximately 20 years ago (Reshef, 1965). All the sheep present in the flock at the time of the survey (195 one to eight years old ewes and 6 two to five years old rams) were examined for their Hb type. Haemoglobin types were determined by vertical starch gel electrophoresis (Smithies, 1955), using borate buffer (gel, pH 8.6).

Sheep are kept indoors under intensive management throughout the year, as described previously (Eyal et al., 1978). Selection for replacement is done using an index in which milk and lamb production are both included and one lamb is considered to be economically equal to 230 litres of milk. Ewe lambs for replacement are obtained from the flock while rams are often brought from commercial flocks. In this flock, the rate of ram replacement is high and on the average five new rams are introduced each year.
Milk yield (as defined by MORAG et al., 1973) was recorded monthly, and in order to arrive at lactation, or annual milk production, the sum of these records was multiplied by 30.

To compare Hb genotypes for milk and lamb production during their first, second and third lactations, least squares analysis of variance by the SAS-GLM procedure was applied. In this analysis, records from all the 21 two to four years old AB ewes and records from 82 of the 90 two to four years old BB ewes were analysed. Data from two years old ewes included information about the first lactation only, while data from four years old ewes included information about three successive lactations. Sources of variation in the analysis were Hb genotype, year and lactation number.

III. Results

The distribution of Hb types and their allelic frequencies in the Newe Ya’ar Assaf dairy flock are shown in table 1. The Hb A frequency in the 195 females was 0.14 and in the six males was 0.25, giving an overall frequency of 0.14 for allele A. No significant differences were found between allele frequencies in the different age groups. Chi-square analysis of the ewe population shows that the genotype distribution does not deviate significantly from Hardy-Weinberg equilibrium, \( P(\chi^2 < 2.8) = 0.24 \).

| Sex | Age (years)* | n  | Hb genotype | P_A  |
|-----|--------------|----|-------------|------|
|     |              |    | AA | AB | BB |     |
| Ewes| 1            | 29 | 1  | 7  | 21 | 0.15|
|     | 2            | 33 | 2  | 6  | 25 | 0.15|
|     | 3            | 34 | 1  | 6  | 27 | 0.15|
|     | 4            | 47 |    | 9  | 38 | 0.10|
|     | 5-6          | 40 | 2  | 10 | 28 | 0.17|
|     | 7-8          | 12 | 1  | 4  | 7  | 0.21|
| Ewes Total |      | 195| 7  | 42 | 146| 0.14|
| Rams | 2-5          | 6  |    | 3  | 3  | 0.25|

* Age at time of Hb survey.

Milk and lamb production in the first, the second and the third lactation were compared between ewes 2, 3 and 4 years old from the AB and BB Hb genotypes (Table 2). Significant differences were found in favour of the AB genotype in the first
lactation both in lambing percentage ($P < 0.03$) and in milk production ($P < 0.01$). An advantage of the $AB$ genotype was evident also in the second lactation; however, here the differences were not statistically significant. In the third lactation milk production and lambing percentage were found to be similar in the two genotypes.

In a small flock all the individuals carrying the rare allele can be the offspring of a common father. In this case deviation from the population mean of this group in performance can be the outcome of sire rather than genotype effect. Pedigree analysis of the flock shows that in the present study, the 21 $AB$ ewes which participated in the analysis are daughters of eight rams.

### IV. Discussion

Three lines of evidence: (i) the very low frequency of $Hb\, A$ allele in the local Awassi breed (EVANS et al., 1958); (ii) the inferior survival ability of Assaf and pure East Friesian ewes carrying $Hb\, A$ in comparison with homozygous $BB$ ewes (RESHEF, 1965; EYAL, 1968); and (iii) the repeated decline in $Hb\, A$ frequency from 0.38 in the $F_1$ to 0.22 in the $F_3$ led to the assumption that $Hb\, A$ frequency will continue to decline, with time, in the Assaf population in Israel.

In the present study, which was done some eight generations after the Hb survey in the $F_3$, the $Hb\, A$ allele frequency calculated was 0.14 indicating a further decline in the allele $A$ frequency. This change in the Hb allele frequency may be due to drift effect. However, the possibility that selection forces are involved, have to be taken into consideration. The further decline in the Assaf breed, of the $A$ allele which originated almost entirely from the East Friesian parental breed, can be explained by the apparently shorter life span of the $A$ allele carriers (RESHEF, 1965; EYAL, 1968). Yet it is evident that the rate of the decline in the later generations was lower than in the first generations.

#### Table 2

| Lambs | Hb genotype | n  | L/E/L | Milk yield/ year (kg) |
|-------|-------------|----|-------|-----------------------|
| First | $AB$        | 21 | 1.56\(^a\) | 266\(^a\)        |
|       | $BB$        | 82 | 1.27\(^b\) | 210\(^b\)        |
| Second| $AB$        | 15 | 1.73   | 300                 |
|       | $BB$        | 65 | 1.53   | 263                 |
| Third | $AB$        | 9  | 1.66   | 261                 |
|       | $BB$        | 34 | 1.71   | 264                 |

Mean in the same square with different superscripts are significantly different ($P < 0.05$).
On the other hand, the AB genotype showed in this study a significant advantage over the BB genotype both in lamb and milk production in the first lactation and possibly also in the second one. A similar advantage in milk production was noted in previous work (Reshef, 1965; Eyal, 1968). Since in the Assaf dairy flocks selection for high milk and lamb production is done usually on the mean production over three or more lactations, carrying the A allele has economic selective advantages. The present allele A frequency in the population, therefore, may be the outcome of the advantage of the AB heterozygotes on AA homozygotes for survival and on BB homozygotes for production. Hence, the AB genotype could serve as an indirect selection criterion for milk and lamb production in the Assaf breed.

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