

Four-Horns, Split Eyelids

by Eric Medway

The Inheritance of Four (Multiple) Horns

Historically, two propositions have been made. Simply, one states that the allele for four horns is dominant, whilst the other suggests it is recessive! Marshall Watson suggests that the four-horned characteristic is produced by the inheritance of a dominant splitting gene (the expression of which will be modified, to a greater or lesser extent by independently inherited modifying genes, see later); all Hebrideans possessing a gene for “horns” of some number. Henson, however, favours a simple Mendelian inheritance for horn number, the two-horned allele being dominant to the allele for four horns. It is all too easy to jump to the conclusion that an unusual characteristic (in this case, four horns) is determined by a recessive allele. In fact, the frequency of the characteristic is also a function of the frequency of the allele responsible in the whole population. If only a few sheep carry the allele for four horns, few four horned lambs will be born, no matter whether the allele is dominant or recessive!

Breeders' experience and the fact that many flocks consist only of two-horned Hebrideans (by breeding only from two horned sheep) suggest that Marshall Watson's theory is correct. To illustrate the point, let us consider the alternative, that the allele for the two-horned condition is dominant, and see how it just doesn't fit the evidence:

In this model there would be two genotypes for two-horned sheep, homozygous (where two dominant alleles for 2-horns are carried) and heterozygous (where the two-horned animal carries one allele for 2-horns and one for 4-horns). Four-horned animals would have to be homozygous recessive, carrying two copies of the allele for 4-horns. If the number of horns is inherited in this fashion then 1 in 4 of the lambs born to two-horned parents who are both heterozygous should be four-horned. With one dubious exception from long ago, there is no record of a four-horned lamb being produced from two-horned parents.

Three years ago, our Flock Survey showed that 11% of more than 1000 sheep were multi-horned. Now, if Hebrideans have not been subjected to excessive inbreeding over the years, one can calculate from this figure that almost exactly half the 2-horned animals would be homozygous and half heterozygous. Thus, one would expect that 1 in 16 of all the lambs born to 2-horned ewes tupped by 2-horned rams would be four-horned! Is this your experience?

Perhaps Hebrideans have been very inbred for many generations and there has been considerable selection against four-horned animals so that now almost all the two-horned animals are homozygous (inbreeding does this). I'm sure this can't be true; such inbreeding would, by now, have shown other, deleterious effects.

It's also the common experience of breeders that a cross between a four-horned animal and a two-horned one is quite likely to produce lambs of both types, showing the two-horned parent to be heterozygous by this model. The rarity of two 2-horned parents producing 4-horned lambs and the common occurrence of 4-horned lambs from mixed parents are contradictions within this model of inheritance.

According to this model, breeding from two four-horned sheep should produce only four-horned lambs. It isn't the case. A number of two-horned sheep are produced as well.

Finally, and perhaps most convincing of all, the ability (and growing trend?) of breeders to keep a flock consisting only of two-horned sheep would be rendered very difficult by this model. A heterozygous two-horned ram would produce about 1 in 4 four-horned lambs with any heterozygous ewes in the flock.

The suggestion made by Marshall Watson looks much safer : the multiple horned characteristic is determined by a dominant splitting allele which causes the horn growth to be divided.

Split Eyelids

This fault has been observed in some multiple horned Hebrideans as well as the other breeds (Manx and Jacob). It may be seen as a small notch in the line of the upper eyelid, or may be as severe as a complete division of the upper eyelid into two parts, making it impossible for the sheep to close the eye properly. This has a considerable welfare implication, especially in dusty or sandy conditions. Anyone who has experience of the western shores of the Hebridean islands when the wind is force 6 or above will readily appreciate this point.

Survey of Inheritance

Some years ago, in response to members' requests, we set up a survey of the incidence of the split-eyelid condition in multi-horned Hebrideans (see Black Sheep No.3). Members had wondered whether it would be possible to eradicate split-eyelids from the breed without seriously depleting the genetic stock of multi-horned animals; earlier evidence (Elizabeth Henson, 1981) had indicated that the fault could be eliminated.

Replies from interested members produced records for 178 multi-horned sheep. The eye condition and horn number of both parents was recorded for 68 of these and details for one parent for a further 79. The parentage of the remaining 31 was unclear and these records have not been included in the analysis. Tables 1 - 3 show the parentage of recorded multi-horned animals of each eye status.

Table 1: 57 Animals with Perfect Eyes

Eye status of	1st Parent					
		P	N	S	2	?
2nd Parent	P	1	6	0	14	23
	N		0	0	8	0
	S			0	1	4

Table 3: 51 Animals with Notched Eyes

Eye status of	1st Parent					
		P	N	S	2	?
2nd Parent	P	4	6	1	7	20
	N		0	0	9	4
	S			0	0	0

Table 3: 39 Animals with Split Eyes

Eye status of	1st Parent					
		P	N	S	2	?
2nd Parent	P	1	10	0	7	8
	N		0	1	3	2
	S			0	0	7

(P = Perfect eyelids; N = Notched eyelids; S = Split eyelids; 2 = 2 horn animal; ? = parent unknown.)

It is important to note that entries of 0 in these tables mean that no animals of such a parentage were recorded; it does not imply that such progeny would be unlikely. To take a specific example, very few animals with split eyelids would ever have been used for breeding, so many zeros in the rows and columns for S would be expected.

Even a brief inspection of these data reveals that 4-horned sheep with perfect eyes are most often the progeny of a perfect-eyed parent. Split-eyed lambs are rarely produced from perfect-eyed parents. (Though with only 6 lambs recorded as the progeny of two perfect parents, this conclusion is difficult to justify statistically.) These results give some support to the conclusions of Henson (1981) based on the suggestion of Marshall Watson (1978) that modifying genes, which are additive, have an epistatic relationship with the splitting gene so as to reduce the severity of its expression. Thus, four-horned sheep with perfect eyes would carry several of these modifiers; those with severe splits would carry few. These modifying genes would also be carried, in various numbers, by two-horned animals and could equally well afford “split-protection” to any four-horned offspring.

Conclusions and Questions

- almost all Hebrideans (some polled included?) carry the gene for “horns”
- some, including polled (and perhaps a very few 2-horned?) carry a dominant gene for “splitting”
- any animal can carry one or more additive “modifier genes”
- these “modifier genes” adjust the expression of the “splitting gene” (when present) to produce a range of phenotypes.
- no “modifiers” allows the splitting gene to produce 4-horns, split-eyelids, perhaps even incomplete fusion of the frontal and parietal bones of the skull
- many “modifiers” suppress the expression of the “splitting gene” to produce perfect eyes, (perhaps even only 2 horns, thus accounting for the very rare event of a 4-horned lamb from 2-horned parents?).

One thing seems certain, selection against animals with defective eyes will gradually reduce this condition from the flock by retaining those sheep with plenty of “modifier genes”. It is easiest to do in flocks where four-horned animals are the majority - but breeders' experience is that occasional use of two horned animals (particularly a strong-horned ram) improves horn quality in four-horned stock. Regard must also be paid to any two-horned parents since they too can contribute modifiers (or not!) - this needs

careful record keeping to allow effective progeny testing. It's important, of course, to keep the whole animal in mind and not to become obsessed about eyelids. A flock of perfect-eyed, four-horned "Hebrideans" with runty bodies, bad mouths, poor fleeces and small udders wouldn't be worth a lot!

References

1. Elizabeth Henson (1981), A Study of the Congenital Defect 'Split Eyelid' in the Multi-Horned Breeds of British Sheep, ARK, VIII, pp84-90.
2. J.M.Watson (1978), Split Eyelids, ARK, V, "Forum", pp428-429.

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