A suggested mode of inheritance for wool shedding in sheep

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ABSTRACT: The ability of a sheep to shed its own wool has an attraction in scenarios where the costs of harvesting wool outweigh its value. Certain breeds and composites have the ability to shed their wool in the spring, and these are investigated in this work in an attempt to outline the genetics of wool shedding. One flock from a breeding group in Southern England (UK) containing sheep with wool-shedding characteristics provided shedding scores (1 to 5 scale; no shedding to complete shedding) that were used in a range of genetic analyses. The particular nature of wool shedding suggested that there may be a major gene segregating in these populations that facilitates wool shedding. In addition, there was clearly variation among wool shedders in the speed and extent of shedding, so a polygenic trait was also investigated. The breeding group used a range of shedding breeds and composites in a regular program to introduce wool-shedding genes into their flocks. This allowed the testing of Mendelian ratios for shedders:nonshedders in both first-cross and first-back-cross animals. Four modes of inheritance were tested: autosomal recessive, sex-linked recessive, autosomal dominant, and sex-linked dominant. The most likely mode of inheritance was autosomal dominant ($P < 0.05$), with a low level of incomplete penetrance. In first back-cross animals, this mode of inheritance was confirmed but with complete penetrance. Approximately 11% of shedders did not exhibit the trait as lambs. Mixed-model analyses of shedding scores allowed an investigation of factors that affected wool shedding and also the extent of any genetic and permanent animal variance. Shedding score was found to have a heritability of $0.54 \pm 0.07$ in lambs and $0.26 \pm 0.06$ in animals of all ages in one flock using Easycare, Wiltshire Horn, Katahdin, and Dorper shedding animals. Shedding score as a lamb had a genetic correlation of $0.94 \pm 0.08$ with shedding score as a 2 yr old, but at the phenotypic level this correlation was only $0.39 \pm 0.05$. No permanent animal effect was found for shedding score. Breeding for increased wool-shedding ability is possible, but improvement of the trait needs to be considered in 2 stages. First, the dominant gene needs to be introduced into the population, and then selection between animals can proceed by using EBV for the polygenic trait (speed or extent of shedding) as the basis for selection. 

Key words: Mendelian genetics, quantitative genetics, sheep, wool shedding

INTRODUCTION

In some countries, the income from wool is a minor part of returns from a sheep flock, and the need to shear animals has a negative effect on farm profitability (Vipond, 2008). Breeding a type of sheep that requires no shearing should reduce costs, a process already underway for traits such as increased parasite resistance (to reduce anthelmintic costs) and unassisted lambing (to reduce shepherding costs). Several breeds are known to possess the ability to shed wool. Primitive sheep breeds shed naturally in the spring, and the prevention of shedding is considered to be one effect of domestication (Ryder, 1981, 1983). Other more domesticated sheep breeds have also been kept partly for their shedding ability (e.g., Wiltshire Horn). New or composite breeds, such as Easycare, Dorper, and Katahdin, have also been bred for their wool-shedding characteristics. Sleek (1959) defined wool shedding as “the absolute loss of fleece, as observed macroscopically, over the whole or any significant part of the body area. This type of shedding should be distinguished from the shedding of individual fibers, which may or may not be sufficiently coordinated and extensive to cause the loss of parts of the fleece” (p. 209). This paper reports a genetic analysis of data from a breeding group in the United King-
dom that set out to breed a type of sheep that sheds its wool by introgressing wool-shedding genes. Several wool-shedding breeds were used in the introgression program, and 2 key characteristics relating to wool shedding were analyzed: the ability to shed and the speed or extent of shedding. The hypothesis proposed in this paper is that the genetic control of wool shedding can, primarily at least, be separated into 2 parts. First, the ability to shed annually is under a simple Mendelian mode of inheritance, and second, the speed or extent of shedding is a polygenic trait that can be seen only in the presence of this major shedding gene.

MATERIALS AND METHODS

The animals used as subjects in this study were kept on a commercial farm and were not subjected to any experimental procedures or treatments.

Wool-Shedding Flocks

Data for this study were derived from 1 flock from a group of breeders with an interest in wool shedding by using sheep comprising a range of shedding and nonshedding breeds [Sheep Improved Genetics Ltd. (SIG, Tiverton, UK)]. All flocks were maintained in the south of England and were recorded for parentage and a range of traits using Signet (Stoneleigh, UK), the British national sheep recording service, and a system operated by Shearwell Data Ltd. (Minehead, UK), as well as records of the breeders. Full pedigree records were available, as well as the details of date of birth, sex, birth type, and BW.

Animals in the SIG group are being used to develop a new breed of sheep by incorporating wool shedding into a composite with a range of key characteristics considered important for economic sheep production. The single flock described in these analyses used Easycare (Easy Care Sheep Society, 2011), Wiltshire Horn (Wiltshire Horn Sheep Society, 2011), Katahdin (Oklahoma State University, 2011), and Dorper (Oklahoma State University, 2011) rams, all wool shedders, in conjunction with several purebred ewes (Friesland, Lleyn, Suffolk, Texel), which are described here as nonshedding breeds. Shedding rams were initially mated to nonshedding ewes to produce a first-cross generation (F1); these F1 animals were then backcrossed to shedding rams in the next generation to produce first-backcross animals (BC1). Both purebred shedding rams and home-produced crossbred rams were then used in subsequent generations on a range of homebred crossbred types, including a further backcross to the original shedding rams (BC2). Selection of replacements was based on several criteria, including wool-shedding ability.

Scoring Wool Shedding

The flocks in the SIG have adopted a 5-point scoring system, shown in Table 1, based on the system of Dolling et al. (1993). Animals were scored annually between May and September (late spring to late summer), beginning in their first year. After initial scorer training, the same scorer was used within any given flock and year. Date of scoring, BW, and shedding score were recorded. The shedding scores were used to classify animals into 1 of 3 types: shedders, nonshedders, and unknown shedding status. Animals were considered to be shedders if they had a score of more than 1 at least once in their recorded lifetime. Animals were considered to be nonshedders if they did not exhibit wool shedding from their second year onward. Lambs not shedding in their first year but not having a further opportunity to be recorded were classed as having unknown shedding status.

Mendelian Analyses

Segregation analysis was carried out on the recorded animals. Mendelian ratios were calculated for shedders:nonshedders for the F1 offspring of shedding rams and nonshedding purebred ewes and for BC1 matings between F1 ewes and shedding rams. Four modes of single-gene inheritance for the ability to shed wool were tested: autosomal recessive, autosomal dominant, sex-linked recessive, and sex-linked dominant. Observed and expected ratios were compared using Fisher’s exact test (SAS Inst. Inc., Cary, NC), and hypotheses were rejected at the 5% level of probability. The expected ratios of shedders:nonshedders for each mode of inheritance are shown in Table 2, and possible BC1 ratios are shown in Table 3, based on an autosomal dominant mode of inheritance.

Quantitative Genetic Analysis

A quantitative genetic analysis was carried out using data from known shedding animals. Mixed animal models were used in ASReml (Gilmour et al., 2009) to

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Table 1. The basic wool-shedding scoring system used in this study

<table>
<thead>
<tr>
<th>Score</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>Wool shed from all the wool-growing area (WGA)</td>
</tr>
<tr>
<td>4</td>
<td>Wool shed from more than 3/4 of the WGA (but some wool still present and not shed)</td>
</tr>
<tr>
<td>3</td>
<td>Wool shed from more than 1/2 but less than 3/4 of the WGA</td>
</tr>
<tr>
<td>2</td>
<td>Wool shed from less than 1/2 of the WGA but evidence of some shedding</td>
</tr>
<tr>
<td>1</td>
<td>No wool shed from the WGA</td>
</tr>
</tbody>
</table>

1Based on Dolling et al. (1993).
investigate environmental and genetic factors that may affect wool shedding. Separate analyses were carried out for shedding records taken on lambs and those on older animals.

**Lamb Analysis**

The following mixed model was fitted to wool-shedding data from the lambs:

\[
W_{ijklmno} = \mu + s_i + d_j + b_k + y_l + g_m + \sum_{n=1}^{2} a_n \cdot n + b_n + e_{ijklmno},
\]

where \( W_{ijklmno} \) was the shedding score of the \( o \)th lamb, of the \( i \)th sex (\( i = 1 \) to 3), from the \( j \)th age of dam (\( j = 1 \) to 4), of the \( k \)th birth type (\( k = 1 \) to 3; gonadally intact male, castrated male, female), born in the \( l \)th year (\( l = 2007 \) to 2010), of the \( m \)th genetic type (breed or crossbred type; e.g., Easycare \( F_1 \)) and scored at age (in days) fitted as a polynomial with regression coefficients \( a_n \) where \( n = 1 \) to 2. Two random effects were included in the model, \( b_n \) and \( e_{ijklmno} \) representing the additive genetic effect and residual error terms, both assumed to be normally distributed, with mean 0 and variances \( \sigma^2_a \) and \( \sigma^2_e \), respectively. The additive genetic variance was calculated using the pedigree relationship matrix. Predicted means within an effect class were compared using a Student’s \( t \)-distribution (Gilmour et al., 2009). Heritability was estimated as the ratio of the lamb effect to phenotypic variance with its SE calculated as described by Gilmour et al. (2009). A further lamb analysis was carried out using a binomial model with a logit link function to investigate the effects that may influence shedding as a lamb. All lambs classed as shedders, based on their lifetime performance, were used in this analysis, and the trait analyzed was shedding score status as a lamb, shedder (1) or nonshedder (0). Equation [1] was fitted to this trait, omitting the additive genetic term.

**Single and Repeat Record Analysis**

To maximize the amount of genetic information for analysis, all animals that had a shedding score were selected, and a single shedding score record from the oldest age possible was used. These data were then analyzed with the following mixed model:

\[
W_{ijklmno} = \mu + s_i + c_j + b_k + y_l + g_m + a_n + e_{ijklmno},
\]

where \( W_{ijklmno} \) was the shedding score of the \( n \)th animal, of the \( i \)th sex (\( i = 1 \) to 3), from the \( j \)th age (\( c \) in years; \( j = 1 \) to 5), of the \( k \)th birth type (\( b \); \( k = 1 \) to 3), born in the \( l \)th year (\( g \); \( l = 2007 \) to 2010), of the \( m \)th genetic type (\( g \)). Two random effects were included in

### Table 2. Expected segregation ratios from crossing nonshedding ewes with shedding rams under 4 modes of single-gene inheritance for wool shedding

<table>
<thead>
<tr>
<th>Male genotype (shedder)</th>
<th>Female genotype (nonshedder)</th>
<th>( F_1 ) offspring genotype</th>
<th>Expected shedder: nonshedder ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>ss</td>
<td>SS</td>
<td>All Ss</td>
<td>0:1</td>
</tr>
<tr>
<td>Sex-linked recessive</td>
<td>SsY</td>
<td>1Ss:1SY</td>
<td>0:1</td>
</tr>
<tr>
<td>Autosomal dominant</td>
<td>SS</td>
<td>All Ss</td>
<td>1:0</td>
</tr>
<tr>
<td>Sex-linked dominant</td>
<td>SY</td>
<td>1Ss:1ss</td>
<td>1:1</td>
</tr>
</tbody>
</table>

\(^1\)S and s denote the dominant and recessive forms of the single gene, respectively; \( Y \) denotes the male chromosome.

### Table 3. Expected segregation ratios from backcrossing first-cross (\( F_1 \)) ewes with shedding rams based on an autosomal dominant mode of inheritance

<table>
<thead>
<tr>
<th>Item</th>
<th>( F_1 ) mother genotype, ram genotype</th>
<th>SS, SS</th>
<th>SS, Ss</th>
<th>ss, SS</th>
<th>ss, Ss</th>
</tr>
</thead>
<tbody>
<tr>
<td>BC1 genotypes</td>
<td>Ss, SS</td>
<td>1:1</td>
<td>Ss:Ss</td>
<td>1:2:1</td>
<td>SS:Ss:ss</td>
</tr>
<tr>
<td>BC1 phenotype ratio of shedders:nonshedders</td>
<td>All Ss</td>
<td>1:1</td>
<td>Ss:ss</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^1\)S and s denote the dominant and recessive forms of the single gene, respectively. BC1 = first backcross.

\(^2\)The ss genotype is possible if the ewe’s sire was Ss.
the model, $a_n$ the additive genetic effect, and $e_{ijklmno}$ the residual error effect, with a mean of 0 and variances $\sigma_a^2$ and $\sigma_e^2$, respectively. Predicted means were compared using Student’s $t$-statistics for all comparisons. The phenotypic variance was estimated as the sum of the 2 random terms. Heritability was estimated as the ratio of the additive genetic variance to the phenotypic variance. All SE were calculated as described by Gilmour et al. (2009). A similar analysis was run on all data from animals older than 1 yr of age to see if the lamb effect differed from that in older animals.

A further analysis was undertaken for all animals having repeated shedding score records. In this case, an extra random term was included in Eq. [2] to account for the permanent environmental effect of the animal. The phenotypic variance was calculated as the sum of the 3 random effects and the repeatability, estimated as the sum of the additive and permanent environmental effects as a proportion of the phenotypic variance.

### Shedding as a Trait of the Lamb and 2 Yr Old

To determine if wool shedding was controlled by the same genes in lambs as in older animals, a data set was constructed of all lambs that also had a record as a 2 yr old. Equations [1] and [2] were used for each age group as appropriate, and the shedding score at each age was treated as 2 separate traits. Both the genetic and phenotypic correlations between shedding score at both ages were calculated as described by Gilmour et al. (2009).

### RESULTS

A summary of the wool-shedding scores for the recorded population is shown in Table 4. The mean shedding score increased from lambs to older animals and its variability reduced with age. Wool-shedding results were available from 1,467 male, female, and castrated lambs born between 2007 and 2010. These are summarized in Table 5 by lamb and lifetime shedding status. The majority of the animals with unknown shedding status were males that had a shedding score of 1 as lambs and were mostly used for meat production, and therefore were not available in their second year for scoring. More important, 82 animals were classified as shedders based on their lifetime performance but did not shed as lambs. Only 15 lambs were true nonshedd-ers, although the number of males that would have fallen into this group was unknown. Taking the female lambs with a known lifetime shedding status, 80 out of 735 (10.9%) did not shed as lambs despite being later known as shedders. Overall, 13 out of 748 (1.7%) female lambs with a known lifetime shedding status turned out to be nonshedd-ers. Applying the same ratio to the lambs with an unknown lifetime shedding status, then there would have been approximately 25 nonshedd-ers among the 1,467 lambs recorded.

The mode of inheritance of wool shedding was inves-tigated using the lamb data from animals with known shedding status. First-cross and BC1 lambs from a shedding-breed sire mated to a nonshedding-breed dam (F1) and an F1 dam (BC1) were used for these analyses. The expected ratios of shedder to nonshedder lambs are shown in Tables 2 and 3. If the mode of inheritance of the shedding gene was either autosomal or sex-linked recessive, then no F1 lambs would be shedders (Table 2). This was clearly not the case (Table 6), and the appropriate ratio (0:1) was tested using a $\chi^2$ test (data not shown for any $\chi^2$ analysis; $\chi^2$ value 144.5, 1 df, $P < 0.001$). The sex-linked dominant scenario was also eliminated because there were both male and female shedders among the F1 lambs (male $\chi^2$ value 5,850, 1 df, $P < 0.001$; female $\chi^2$ value 101, 1 df, $P < 0.001$).

Testing the autosomal dominant mode of inheritance against the expected 1:0 ratio of shedders:nonshedders resulted in a significantly different ratio than expected ($\chi^2$ value 13.6; $P < 0.001$), and the remaining question concerns the genotype of the rams used (homozygous or heterozygous for this dominant gene). The occurrence of shedding in F1 lambs by sire is shown in Table 7. No sire group had a 1:1 ratio of shedders to nonshedders (all $\chi^2 P < 0.001$) and even if the lambs of unknown

<table>
<thead>
<tr>
<th>Age, yr</th>
<th>Number</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1,467</td>
<td>2.6</td>
<td>1.30</td>
</tr>
<tr>
<td>1</td>
<td>585</td>
<td>3.4</td>
<td>1.30</td>
</tr>
<tr>
<td>2</td>
<td>306</td>
<td>3.3</td>
<td>1.27</td>
</tr>
<tr>
<td>3</td>
<td>119</td>
<td>3.5</td>
<td>1.17</td>
</tr>
<tr>
<td>&gt;3</td>
<td>50</td>
<td>3.5</td>
<td>0.89</td>
</tr>
<tr>
<td>Total</td>
<td>2,527</td>
<td>2.9</td>
<td>1.28</td>
</tr>
</tbody>
</table>

**Table 5.** Incidence of lamb shedding scores by shedding status and sex of lamb

<table>
<thead>
<tr>
<th>Lamb shedding</th>
<th>Nonshedder</th>
<th>Shedder</th>
<th>Unknown</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Female</td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td>Nonshedder</td>
<td>13</td>
<td>2</td>
<td>80</td>
</tr>
<tr>
<td>Shedder</td>
<td>190</td>
<td>655</td>
<td>361</td>
</tr>
<tr>
<td>Total</td>
<td>13</td>
<td>2</td>
<td>190</td>
</tr>
</tbody>
</table>

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shedding status were added to the nonshedders, only Easycare ram 4 would have had a 1:1 ratio. Because this ram left only 4 lambs in total, its result provides no evidence to support any given mode of inheritance. Further evidence for the mode of inheritance of the wool-shedding gene can be gained from the BC1 data shown in Table 8 and the expectations of shedding status shown in Table 3. Out of the 684 BC1 lambs with known shedding status, only 1 was classified as a nonshedder. This implies that all rams used in the backcross were likely to be homozygous for the shedding gene (all $\chi^2$ values $P < 0.001$; Table 3), and it seems likely that an autosomal dominant gene is acting in this population to “turn on” wool shedding. A small number of anomalous animals are apparent if this mode of action is correct. Thirteen F1 lambs did not shed, and these were also used as BC1 dams.

### Shedding Scores Recorded for the Same Animal

Wool-shedding scores of known shedders were recorded for the same animals in different years. Figures 1 and 2 show the relationship between the wool scores of the same animal in successive years as a lamb and a 2 yr old (Figure 1), and as a 2 yr old and a 3 yr old (Figure 2). These 2 relationships differed. Lambs with a decreased score (<3) tended to have greater scores a year later, but lambs with scores between 3 and 5 averaged approximately 4 as 2 yr olds; the overall correlation between score as a lamb and as an older animal was $0.51 \pm 0.035$. A much smaller correlation was observed between scores at successive older ages ($0.25 \pm 0.06$).

### Quantitative Analysis of Shedding Score

This part of the study concentrated on the shedding characteristics of animals known to be wool shedders and can be thought of as reflecting the speed or extent of shedding during the summer. Only animals known to be shedders were used for these analyses. For the 3 data sets analyzed, a pedigree file of all animals in the flock was constructed back to all known ancestors. For the 1,680 animals with wool-shedding scores, this constituted 2,018 individuals.

### Lamb Analyses

A mixed-model analysis was performed on 1,288 lamb wool-shedding scores from animals confirmed as shedders. Age (in days fitted as a second-order polynomial), sex, birth type, year of birth, and genetic type were all found to affect wool-shedding score ($P < 0.001$ in all cases), but dam age did not ($P > 0.05$). The predicted means for sex indicated that females had a greater shedding score than intact males (data not shown for all comparisons; 3.19 vs. 2.77, $P < 0.05$) and castrates (2.97, $P < 0.05$), but males and castrates were similar ($P > 0.05$). Single-born lambs had greater shedding scores than twins (3.26 vs. 2.88, $P < 0.05$) and triplets (2.70, $P < 0.05$), but twins and triplets were similar ($P > 0.05$). Shedding score increased with age of the lamb, from 2.2 at 80 d to a plateau of 2.99 at 200 d. Genetic-type effects ranged from 1.76 for the Katahdin F1 lambs to 3.82 for the Easycare BC2 lambs. The heritability of shedding score was $0.45 \pm 0.08$ when breed type was...
The binomial analysis of shedding as a lamb indicated that sex, genetic type, and age at scoring were all significant factors ($P < 0.01$). A reduced amount of shedding was observed for female lambs, compared with the other sexes, and shedding increased with age at shedding in these lambs. The various F$_1$ types of lamb also showed less of a tendency to shed as a lamb compared with the other genetic types.

### All-Animal Analyses

Equation [2] was fitted to 1,485 records of animals of all ages. All fixed effects significantly influenced wool-shedding score ($P < 0.001$). Lambs had smaller shedding scores than older animals (2.57 vs. 2.77; $P < 0.05$), but no differences were observed between older age groups ($P > 0.05$). Single-born animals had greater shedding scores than twins or triplets (2.67 vs. 2.42; $P < 0.05$), but multiple-born animals were not distinguishable from each other. Females had greater shedding scores than both types of males (intact and castrate; 3.02 vs. 2.39; $P < 0.05$). Shedding score increased through the progression from Easycare F$_1$, BC$_1$, and BC$_2$ (2.56 v 3.16 vs. 3.36; $P < 0.05$), and the Katahdin and Dorper F$_1$ had smaller scores than the Easycare F$_1$ (2.00 vs. 1.93 v 2.56; $P < 0.05$). The heritability of shedding score was 0.10 ± 0.05 when breed type was included in the model and was 0.26 ± 0.06 when it was excluded. When the analyses were rerun using only data from animals older than 1 yr of age, then the effects of sex and birth type were nonsignificant and the heritability was little affected, at 0.27 ± 0.10.

In the repeatability analysis, Eq. [2] was fitted to 1,390 records from 580 shedding animals with repeated records. All fixed effects fitted had a significant effect on shedding score ($P < 0.001$; $P < 0.05$ in the case of sex) except birth type ($P > 0.05$). The predicted means of these effects were similar to those reported for the single-record analysis. Both the heritability and repeatability of shedding score was 0.16 ± 0.04 when genetic
type was fitted to the data and was 0.23 ± 0.03 when it was ignored in the model; the permanent environmental effect was zero.

The genetic and phenotypic correlations between shedding score as a lamb and shedding score as a 2 yr old were 0.94 ± 0.08 and 0.39 ± 0.05, respectively, indicating that genetically they were almost the same trait.

**DISCUSSION**

With wool production being a major economic driver in several countries, it is not surprising that wool shedding has been studied previously, but in such situations, it is commonly seen as a negative factor. One exception to this was reported by Rathie et al. (1994), who investigated various Merino crosses with Wiltshire Horn rams in an attempt to reduce fly strike.

The natural process of wool shedding has been documented by several authors and with several shedding score systems in the literature. Slee (1959) used a 10-point scale relating to the percentage of body area having lost its fleece, whereas in Slee (1963), this was expanded to a 20-point scale. The 10-point scale was used by Gatenby et al. (1997) in their study of Sumatran sheep. Pascoe et al. (1976) classified 5 areas of the body into completely shed, not shed, and partially shed as the basis for their breed comparison. Archer et al. (1982) appear to be the first to use a 5-point scoring system applied to 6 regions of the body, with smaller scores indicating less fleece cover. This was reversed by Merrick (2003) such that larger scores indicated more wool shedding.

This paper has attempted to explore the genetics of wool shedding in sheep kept in flocks in which wool shedding was encouraged. At the outset, it may be necessary to distinguish between animals that shed their wool because of an innate ability from those that do so as a result of other stimuli. Slee (1959) lists these external stimuli as poor nutrition, overnutrition, health, and, possibly, hormonal in origin. Clearly, breeds exist that shed their wool annually in the spring. The Wiltshire Horn is the most widely used modern breed in this context although primitive breeds also show this wild-type characteristic (Ryder, 1981). Several composite breeds have been developed that incorporate Wiltshire Horn genes and that have been bred to shed their fleece. Because wool shedding runs in breeds, this suggests that the ability to shed is under genetic control, an idea that most authors have found either explicitly or implicitly. Slee (1959) and Slee and Carter (1962) made constant references to genetic control although they did not carry out any specific genetic analysis of wool shedding. Williams (1981), working with Wiltshire Horn F₁ animals in Australia, noted a difference between types in the speed of shedding. No explicit genetic analysis of wool shedding exists in the literature, but Odenya (1982) reported a coat score for Dorper/Massai purebreds and crossbreds. This was analyzed by dam-daughter regression to give a heritability of 0.27 ± 0.11. The real question about the genetics of wool shedding is probably about the mode of inheritance rather than whether it is under genetic control. As Slee (1959) commented, “The ability to shed and the extent of shedding are grossly affected by genotype, but the time of onset of shedding is not” (p. 211). The hypothesis proposed in this paper is that the genetic control of wool shedding can, at least primarily, be separated into 2 parts. First, the ability to shed annually is under a simple Mendelian mode of inheritance, and second, the speed or extent of shedding is a polygenic trait that can be seen only in the presence of this major shedding gene (referred to hereafter as the “shedding switch gene”).

The speed and extent of shedding are grouped together in this study because shedding was measured only once per year on each animal. Wool shedding has been demonstrated to begin in spring and to be a progressive phenomenon with a bilaterally symmetrical pattern. The process starts ventrally, near the axilla, and on the underside of the neck and belly, and it extends evenly dorsally. The saddle and rump areas are usually the last to shed (Slee, 1959). A single shedding score taken once a year means that the spread of shedding (shedding score) and the speed of shedding are not separable. In one instance, a group of ewes were scored approximately 3 wk apart and demonstrated an increase of 0.6 in the score over that period; different breed types exhibited different rates of shedding in these animals. There is also a question of whether shedding as a lamb is the same trait as shedding at older ages.

### Mode of Inheritance of Wool Shedding, Mendelian Trait

The analysis of Mendelian ratios of shedders to nonshedders suggests a dominant mode of inheritance for the shedding switch gene in the animals derived from the Wiltshire Horn, its composites (of which the Easycare breed is an example), and the Dorper composite. The logic for this idea is as follows. All Wiltshire Horn animals shed their fleece, whereas most other breeds (e.g., Suffolk) do not, except under some environmentally stressful circumstances. When an F₁ is produced between a breed of each shedding type, all animals shed their fleece. If shedding ability were a threshold trait under polygenic control, then approximately one-half of the F₁ offspring would be nonshedders. This was not the case, so the ability to shed must be under the control of a small number of genes. Taking single-gene models, then the F₁ data had a ratio of 20:1 shedders to nonshedders. This ratio was different from the 0:1 ratio expected under both the sex-linked and autosomal recessive modes of inheritance, and was also different from the 1:1 ratio expected under a sex-linked dominant mode. Although the F₁ results are not decisive in confirming the autosomal dominant mode of
inheritance for a wool-shedding switch gene, the BC₁ results add considerable weight to the concept. In addition, none of the rams used appeared to be heterozygous for this gene, so the F₁ animals appear to have a low level of incomplete penetrance.

No other report of work testing Mendelian ratios of this trait exists, but Slee (1959) and Slee and Carter (1962) provide some supporting evidence for this concept. Slee (1959) used a variety of Wiltshire Horn and Scottish Blackface crosses to investigate wool shedding in both lambs and ewes. The χ² values shown below were computed from the data of Slee (1959) using Fisher’s exact test in SAS against the expected ratios shown.

In Slee (1959), all purebred Wiltshire Horn lambs shed, whereas none of the Scottish Blackfaces did (Table 2 in Slee, 1959). No lamb results for F₁ animals were quoted, but 93% of BC₁ (χ² = 5.36; P = 0.033 for 1:0 expectation) and 90% of BC₂ (χ² = 1.11; P = 0.61 for 1:0 expectation) lambs shed. It is interesting that 46% of F₂ animals shed, indicating segregation of the nonshedding recessive gene, although not in the 3:1 ratio of shedders to nonshedders that might be expected under autosomal dominance (χ² = 14.02; P < 0.01). Table 3 in Slee (1959) identifies adults recorded in 1954 that showed shedding in 100% of BC₁ and F₂ animals (χ² = 8.0; P = 0.008 for 3:1 expectation), in 93% of F₁ animals (χ² = 4.30; P = 0.061 for 1:0 expectation), and in 13% of Scottish Blackface BC₁ animals, again not the 1:1 ratio expected (χ² = 14.4; P = 0.002). Using a more extensive, but less accurate, data set from 1952 to 1955 Slee (1959) demonstrated that 20% of F₂ animals and approximately 15% of 176 F₁ animals were nonshedders.

Does the evidence from this analysis by Slee (1959) contribute to the concept of a dominant wool-shedding switch gene? Results from the adult data for F₁, F₂, and BC₁ animals all demonstrate an autosomal dominant mode of inheritance. Slee (1959) did not report on the shedding status of the lambs when they became adults, but if we assume that a certain number of lambs carrying the gene did not express it in their first year, then the lamb data also tentatively confirm the hypothesis of a dominant mode of inheritance. Only 7% of the BC₁ lambs did not shed, and the BC₂ animals shed as expected.

Results of Rathie et al. (1994) and Pascoe et al. (1976) add little to the idea that a shedding switch gene exists in Wiltshire Horn-based animals. Rathie et al. (1994) did not separate the results of shedders and nonshedders, but Pascoe et al. (1976) indicated that all Wiltshire Horn F₁ animals showed some evidence of shedding. It is interesting to note that Ryder (1978) reported that none of the 16 F₁ Wiltshire Horn X Wensleydale sheep showed any sign of wool shedding.

Combining all the evidence together, there is good support for wool shedding being initially controlled by a single gene, and both sex-linked and recessive can be rejected as the likely mode of inheritance. Evidence from all sources indicates that a large proportion of F₁ animals from the mating of a wool-shedding ram and a nonshedding ewe shed their wool. Further evidence from backcrosses and, to some extent, F₂ animals confirms that a dominant gene is working to facilitate wool-shedding activity in the majority of animals. Clearly, a minority of animals exist in which this does not happen as expected; genes like this are traditionally referred to as having incomplete penetrance. In particular, lambs do not always appear to express the gene, and some environmental factors may exist that influence their ability to shed.

**Mode of Inheritance of Wool Shedding, Polygenic Trait**

Variation clearly exists in the speed or extent of wool shedding within animals that possess the putative shedding switch gene. In these analyses, several factors have been shown to affect wool shedding, including the additive genetic effect and breed or cross type, as well as a range of external factors. The heritability of shedding score was found to be high in lambs (0.55) but to be somewhat less in older animals, at 0.26. In a separate study, data were available from 243 pedigree Wiltshire Horn animals born in 10 flocks between 2008 and 2009. These animals were scored at approximately 14 mo of age, and the heritability of the shedding score was found to be 0.41 ± 0.20 (G. E. Pollott, unpublished data). It is interesting that where repeated records had been taken on animals in different years, there appeared to be no permanent animal effect on wool shedding over and above the additive genetic effect.

Some of the genetic variation appeared to be due to the different breed or cross types in the shedding population, which can be summarized as follows: The greater the proportion of genes from shedding breeds in a particular cross, the greater the shedding score. This type of result was also found by Rathie et al. (1994), who used different proportions of Wiltshire Horn genes with Merinos: The greater the proportion of Wiltshire Horn genes, the greater the wool-shedding score. In addition, some evidence of differences existed among the shedding breeds, with Wiltshire Horn-based animals having greater scores than Katahdin and Dorper animals. Evidence of a breed effect was found by Merrick (2003), working with a range of breeds in New Zealand scored several times for fleece cover up to 50 wk of age. It is interesting that the Dorper did not appear to confer wool shedding on its offspring in this data set, but otherwise, Wiltshire Horn-based types tended to exhibit greater wool-shedding ability than other breeds. Pascoe et al. (1976) compared a range of F₁ animals from Wiltshire Horn ram crosses. They too noted some differences between breeds in the speed or extent of shedding, but in this case, the differences were between the nonshedding breeds: the Border-Leicester cross with...
Merino and the Corriedale crosses shed faster than the Merino or Southdown crosses. This is notable because it indicates that nonshedding breeds must carry genes that affect wool shedding, even though they do not carry the switch gene required to initiate the process. Further evidence for this was provided by Slee (1959), who commented on purebred Scottish Blackface sheep, a nonshedding breed, showing that when these animals shed because of poor weather conditions, there was a tendency for the same sheep to shed whenever this occurred. This may be tentative evidence to show that even among nonshedding breeds, the tendency to shed is genetically controlled, but they may need another stimulus to initiate shedding.

**Lambs vs. Older Animals**

Some evidence exists that shedding as a lamb may be a somewhat different trait from shedding as an older animal. Not all known shedders exhibited the trait as lambs, and the heritability of wool shedding was greater in lambs than in older animals. However, in the analysis presented here, when treating shedding as a lamb and as an older animal as 2 different traits, the genetic correlation between them was approximately 0.9. This would tend to indicate that shedding at both ages is essentially the same trait, even though at the phenotypic level, the correlation was only approximately 0.4. The correlations between shedding scores at different ages, uncorrected for fixed effects, were 0.5 (lamb vs. second year) and 0.25 (second vs. third year).

Clearly, several additional factors influence the ability of a lamb to express the wool-shedding switch gene that it is carrying. Slee (1963) discusses this at length and considers factors such as date of birth, age of the lamb, and a seasonal environmental factor as being possible causes of variation in shedding. Shedding is clearly seasonal, so it is likely to be associated with a set of factors that change with season. Slee (1963) was unable to detect an effect of sex, birth coat type, or follicle characteristics on lamb shedding ability; in fact, all follicle types were affected similarly. However, Slee (1963) did study age or date of birth and BW characteristics extensively and concluded that a threshold effect of BW existed and that a seasonal effect existed that triggered the onset of shedding in lambs. In the current analysis, some effect of age on shedding ability as a lamb (among shedders) was found and no effect of BW could be detected. It was not possible to substantiate the model in Slee (1963) for lamb shedding because of the tight pattern of lambing dates in the current data set. The mechanism that prevents a lamb carrying the shedding switch gene from shedding in its first year is still largely unknown.

**Breeding for Wool Shedding**

Breeders interested in increasing wool shedding in their sheep need to approach the task at 2 levels. Initially, the introduction of genes from a known wool-shedding breed will create the possibility of making progress. Because of the mode of inheritance of the switch gene, any animals showing wool-shedding tendencies will be carrying at least 1 copy of the gene. However, 2 situations exist in which a genetic test for the gene may be useful: to identify lambs that do not shed but that carry the gene, and to identify the genotypic status of shedders (homozygous or heterozygous). This latter case will not be so important if a policy of backcrossing to a shedding breed is pursued. Once shedding is established in the flock, then further selection will be possible to increase the speed or extent of shedding. Because of the polygenic nature of this aspect of shedding, it is possible to estimate breeding values for shedders and to select in the usual way. Clearly, if other traits also need to be included in the breeding goal, then the use of a selection index, or at least the presentation of breeding values for all the traits, will be required. Although not investigated in detail in this work, it may be possible to identify breeds, both shedding and nonshedding, that have the ability to shed faster or more extensively. The use of such breeds would be an advantage, but only if their other characteristics were found to be useful. Because shedding is a progressive process, the question arises as to the best time of year to record shedding scores. The recommendation to the breeding groups used in this study was to have a spread of scores across the range at the time of recording. In known shedding groups, animals should be scored when approximately 20% reach a score of 5. In a mixed group of shedders and nonshedders, this should be reduced to approximately 15% but will depend on how many nonshedders are expected. In lambs, approximately 10% should be at a score of 5 at the time of recording.

**LITERATURE CITED**


