Divergent selection for fleece weight in French Angora rabbits: Non-genetic effects, genetic parameters and response to selection

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Abstract

In order to explore genetic variability of wool production and other quantitative traits, an 8-cohort divergent selection experiment for total fleece weight (TFW) was carried out in French Angora rabbits. Studies were made on the wool production of 669 female rabbits born between 1994 and 2001 and having produced wool from the third to 12th harvests. The aim of the selection experiment was to obtain two divergent lines (low and high) on total fleece weight. The studied traits included total fleece weight, weight of the two qualities of wool (WAJ1 and WAW1), homogeneity (HOM), live body weight at ages of 4 (LW4), 8 (LW8), 12 (LW12), 16 (LW16), and 20 (LW20) weeks and then 9 weeks before each harvest (9LW). A preliminary analysis of non-genetic factors was done with the GLM procedure. The genetic parameters and genetic trends were analysed using a BLUP animal model. Heritability estimates for TFW, WAJ1, WAW1, HOM, LW4, LW8, LW12, LW16, LW20 and 9LW were 0.38, 0.30, 0.10, 0.06, 0.30, 0.09, 0.14, 0.32, 0.39 and 0.45, respectively. Genetic and phenotypic correlations between TFW and WAJ1 were high (0.98±0.01 and 0.89±0.01, respectively). There was a low genetic correlation between TFW and 9LW (0.26±0.12). After eight cohorts of selection, the divergence between the lines was approximately three genetic standard deviations. Selection for total fleece weight had a generally beneficial effect on fleece quality.

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1. Introduction

The French Angora rabbit breed has a fleece with well-differentiated guard hair (Rougeot and Thébault, 1983) and produces long and bristly wool. Such bristly fleeces are valuable because of their aptitude to produce a fluffy yarn used for certain luxury knit products (Rougeot and Thébault, 1984). World Angora production was approximately 8000 metric tons in 2000 (Schlink and Liu, 2003).

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The opportunity for selection on a trait depends on the amount of additive genetic variation in a trait. Realised heritability has been traditionally estimated by using either a directional or divergent selection design (Hill, 1972). Mixed model methodology and computational resources, however, allow the inclusion of data on all generations and relationships by using an animal model, which has become the method of choice to analyse selection experiments (Sorensen and Kennedy, 1986).

In order to explore the genetic variability of wool production and other quantitative traits in the Angora rabbit, a divergent selection for a trait experiment on total fleece...
weight was undertaken. The experiment began in 1994 and, by 2001, two large cohorts were available from the high and low lines. There is little information on genetic parameters of wool quality in Angora rabbits. This paper reports non-genetic factors affecting wool production and live weights as well as genetic parameters, direct and correlated responses in the lines, measured in female French Angora rabbits over 8 years of a divergent selection experiment.

2. Materials and methods

2.1. Animals

Data were obtained from the Angora experimental rabbit farm of INRA (Institut National Recherche Agronomique) at Le Magneraud, France. The experiment took place in a naturally lighted semi-open building with no heating and no forced ventilation. Rabbits were fed a commercial pelleted diet. Allain et al. (1999) described the management, reproduction and housing circumstances of these animals.

Eight hundred ninety-six rabbits out of a total of 3567 animals born in the herd with full pedigrees recorded were measured. Studies were made of the wool production of 669 female Angora rabbits born between 1994 and 2001 under a divergent selection experiment that was initiated in 1994. French Angora bucks are known to produce 20% less wool than does (Rochambeau et al., 1991). Moreover since the Angora doe’s capacity to foster appears to be limited, French breeders carry out selection at birth according to sex, so that only newborn does and a few bucks are kept (Rougeot and Thébault, 1983). Thus the number of males available was low and statistically insufficient for use in the study. Therefore, only data from females were analysed in the present work.

The aim of the selection experiment was to obtain two divergent lines on total fleece weight (TFW). A high line and a low line were made up of 80 females and 20 males each. Rabbits were distributed between the lines in order to have the same demographic structure and the same distribution of genetic values. Generations were overlapping. The renewal after selection was composed each year of 36 females and 5 males, alive at the second harvest in each line. The selection criterion was the total fleece weight of the does measured for the third and later harvests. During the selection experiment, genetic values were estimated with a BLUP applied to an animal model using MODANIM software (Poivey, 1986). The evaluation of the animals was done each year. Heritability and repeatability were set to 0.31 and 0.51, respectively. Twenty does and five bucks having the highest and the lowest genetic values in the high and the low lines respectively were used for the renewal. The does were inseminated a few days after harvests between the third and the seventh harvest, then after each one. Individual does were limited to six daughters and one son used as replacements. The males born 1 year were used the following year for reproduction. Each of the five bucks was replaced by one of its sons. This pattern of selection was followed for the 8-year duration of the experiment.

2.2. Traits

The young rabbits were sexed at birth and most of the males were eliminated. In this way the size of the litters were reduced to less than six rabbits just after birth. They were weaned 4 weeks later. They were plucked for the first and second times at the ages of 8 and 21 weeks, respectively. Thereafter they were plucked at regular intervals every 14 weeks.

During each wool harvest, the fleece was sorted and graded in five different classes, according to quality: Class 1: clean, unfelted, long and bristly fibre, from the back, the sides and the rump of the rabbit (WAJ1); Class 2: clean, unfelted, long and woolly fibre, from the breast and the belly of the animal (WAW1); Class 3: clean, unfelted and short (<6 cm) fibre, from the legs of the rabbit; Class 4: clean and felted fibre, from the neck and the tail of the animal; Class 5: dirty fibre, from the belly of the rabbit. Homogeneity (HOM) was calculated as the ratio of WAJ1 to TFW, expressed as a percentage. Live body weight at ages of 4 (LW4), 8 (LW8), 12 (LW12), 16 (LW16), and 20 (LW20) weeks were collected. Thereafter animals were weighed at regular intervals 9 weeks before each wool harvest (9LW).

2.3. Statistical analyses

2.3.1. Testing of fixed effects

From preliminary analysis, the dataset was separated into three subsets according to the harvest number: one for each of the first two harvests and one for the third to the 12th harvests. Only fibre data of the third to the 12th fleece harvests were analysed. The least square means method with the GLM procedure was utilised to determine the significance of the fixed effects and covariate.

2.3.2. Estimation of genetic parameters and breeding values

All analyses for genetic parameters and breeding values were carried out with ASReml (Gilmour et al., 2002). In selection experiments with overlapping generations, a mixed model approach shows considerable
advantages over the least-squares estimator (Sorensen and Kennedy, 1986). The method enabled the inclusion of different fixed effects, covariate and random effects in the model for each trait. For fibre traits, a series of bivariate model analyses were first run to estimate covariance components, which were subsequently applied to a multi-trait model to derive genetic and phenotypic correlations among traits. Finally, a multi-trait model was included for TFW, WAJ1, WAW1 and HOM. The following linear mixed model for a multivariate analysis of TFW, WAJ1, WAW1 and HOM traits was used:

$$Y_i = X_i\beta_i + Z_i a_i + W_i p_i + e_i$$

Where

$N$ is the total number of animals,

$N_i$ is the number of animals measured for the $i$th trait,

$Y_i (N_i)$ is a vector of animal records for the $i$th trait,

$\beta_i (f_i)$ is a vector of fixed effects for the $i$th trait consisting of:

- A covariate effect of 9LW on TFW, WAJ1 and WAW1 traits,
- Year (8 levels) from 1994 to 2001,
- Harvest number (10 levels) from the third to the twelfth harvest,
- Birth season effect (4 levels),
- Harvest season effect (4 levels),
- Reproduction (3 levels: females which had litters and females which had been inseminated or not) from the third harvest onwards.

$a_i (N_i)$ is a random vector of direct additive genetic effects of animals for the $i$th trait.

$p_i (N_i)$ is a random vector of permanent environmental effects of animals for the $i$th trait.

A bivariate analysis between 9LW and TFW was undertaken according to the above linear mixed model but without an effect of harvest season for 9LW and covariate for TFW.

For LW4, LW8, LW12, LW16 and LW20, a set of bivariate analysis between body weight and TFW was undertaken. The linear mixed model included the same fixed and random effects as above without covariate for TFW. The vector of significant fixed effects for LW4, LW8, LW12, LW16 and LW20 consisted of Year (8 levels) from 1994 to 2001; Harvest season (4 levels) except for LW4; Age of dam effect (6 levels) for the LW4 trait only; Number of weaned rabbits (6 levels; 1, 2, 3, 4, 5 to 7 and more than 7). A random vector of a common litter environmental effect of animals for LW4, LW8, LW12, LW16 and LW20, was included.

Breeding values for all the traits were obtained as solutions from the best linear unbiased prediction analysis of the ASReml package. Then the means of the estimated breeding value (EBV) for all traits were calculated per cohort of animals born the same year and per selected line.

3. Results and discussion

3.1. Means and standard deviations

Means and standard deviations (S.D.) for total fleece weight (TFW), weight of bristly wool (WAJ1), weight of woolly wool (WAW1), homogeneity (HOM) and live body weights are given in Table 1.

### Table 1: Number of records ($N$), mean and standard deviation (S.D.) for the studied traits: total fleece weight (TFW), weight of bristly wool (WAJ1), weight of woolly wool (WAW1), homogeneity (HOM), live body weight at 4 (LW4), 8 (LW8), 12 (LW12), 16 (LW16), 20 (LW20) weeks of age and 9 weeks before harvest (9LW)

<table>
<thead>
<tr>
<th>Trait</th>
<th>Unit</th>
<th>$N$</th>
<th>Means</th>
<th>S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fibre traits</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TFW</td>
<td>g</td>
<td>3351</td>
<td>214.3</td>
<td>57.2</td>
</tr>
<tr>
<td>WAJ1</td>
<td>g</td>
<td>3351</td>
<td>149.3</td>
<td>46.8</td>
</tr>
<tr>
<td>WAW1</td>
<td>g</td>
<td>3351</td>
<td>30.7</td>
<td>15.3</td>
</tr>
<tr>
<td>HOM</td>
<td>%</td>
<td>3351</td>
<td>69.1</td>
<td>9.3</td>
</tr>
<tr>
<td>Live body traits</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LW4</td>
<td>g</td>
<td>792</td>
<td>597.9</td>
<td>122.6</td>
</tr>
<tr>
<td>LW8</td>
<td>g</td>
<td>736</td>
<td>1364</td>
<td>232.8</td>
</tr>
<tr>
<td>LW12</td>
<td>g</td>
<td>700</td>
<td>2174</td>
<td>294.1</td>
</tr>
<tr>
<td>LW16</td>
<td>g</td>
<td>681</td>
<td>2732</td>
<td>334.0</td>
</tr>
<tr>
<td>LW20</td>
<td>g</td>
<td>630</td>
<td>3003</td>
<td>313.6</td>
</tr>
<tr>
<td>9LW</td>
<td>g</td>
<td>2925</td>
<td>3802</td>
<td>474.0</td>
</tr>
</tbody>
</table>

3.2. Non-genetic effects

Significance levels of fixed effects for fibre traits and 9LW are shown in Table 2. In this study the total weight

### Table 2: Significance levels of fixed effects for total fleece weight (TFW), weight of bristly wool (WAJ1), weight of woolly wool (WAW1), homogeneity (HOM) and live body weight 9 weeks before harvest (9LW)

<table>
<thead>
<tr>
<th>Traits</th>
<th>Fixed effects</th>
<th>Birth season</th>
<th>Harvest season</th>
<th>Reproduction</th>
<th>Covariate</th>
</tr>
</thead>
<tbody>
<tr>
<td>TFW</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>9LW</td>
</tr>
<tr>
<td>WAJ1</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>9LW</td>
</tr>
<tr>
<td>WAW1</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>9LW</td>
</tr>
<tr>
<td>HOM</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>9LW</td>
</tr>
<tr>
<td>9LW</td>
<td>**</td>
<td>***</td>
<td>ns</td>
<td>***</td>
<td></td>
</tr>
</tbody>
</table>

*** $P<0.001$; ** $P<0.01$; * $P<0.05$; ns: non-significant.
of harvested wool increased rapidly from the third to the fourth harvests, remained high from the 4th to the 9th harvest and decreased thereafter (Fig. 1). The observed increase of total fleece weight from the third to the fourth harvest, and then the decrease of total weight of wool in the last three harvests, were similar to earlier results (Rochambeau and Thébault, 1990). An important birth season effect was observed on TFW, WAJ1 and WAW1. The animals born in the summer produced less wool than those that were born in other seasons. The effect of the season of birth, previously demonstrated on hair production in the vole (Lee and Zucker, 1988) and on wool production in angora rabbits (Thébault et al., 1992) was confirmed in the present study.

There was a clear harvest season effect with a higher wool production in the winter than in the other seasons for TFW and WAJ1. The quantity of wool produced varied with the harvest season with a maximum in the winter in agreement with previous observations indicating that the seasons of maximum fleece growth were always the autumn and winter (Caro et al., 1984; Thébault et al., 1992). Rougeot and Thébault (1983) in a study on seasonal variation of wool traits concluded that the weight of the angora wool is minimal in the summer, maximum in the autumn and in the winter and intermediate in the spring.

The values of TFW, WAJ1, WAW1 and HOM in does that had a litter between two harvests were the smallest ($P<0.01$). Does that had been inseminated artificially without producing a litter had a smaller TFW and WAJ1 than does that had not been inseminated ($P<0.05$). The depressive effect of reproduction on live weight and TFW observed in does producing a litter was similar to that found in a previous study (Rochambeau et al., 1991). The difference in wool production between females that had or had not been inseminated can be explained by pseudo pregnancy induced by the hormonal treatment used with artificial insemination.

Significance levels of fixed effects on live body weight traits up to 20 weeks of age are reported in Table 3. Year, birth season and litter size weaned effects were significant on LW8, LW12, LW16 and LW20 traits. For LW4, the effects of year, litter size weaned and age of dam were significant.

### 3.3. Heritabilities and correlations

Table 4 shows the current estimates of phenotypic and genetic parameters for fibre traits. Heritability estimates for TFW were in agreement with other estimates, ranging from 0.31 to 0.42 (Allain et al., 1999; Lin et al., 1995). Youzhang and Pin (1997) obtained heritability estimates of 0.30 and 0.13 for total wool

<table>
<thead>
<tr>
<th>Traits</th>
<th>Fixed effects</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Year</td>
</tr>
<tr>
<td>LW4</td>
<td>***</td>
</tr>
<tr>
<td>LW8</td>
<td>***</td>
</tr>
<tr>
<td>LW12</td>
<td>***</td>
</tr>
<tr>
<td>LW16</td>
<td>***</td>
</tr>
<tr>
<td>LW20</td>
<td>***</td>
</tr>
</tbody>
</table>

*** $P<0.001$; ns: non-significant.
production and percentage of coarse fibres in Angora rabbits, respectively. Genetic and phenotypic correlations between TFW and WAJ1 were positive and highly favourable. WAJ1 is an important economical trait in angora production but its measurement is more difficult and subjective than TFW and the heritability estimate of WAJ1 is lower than that of TFW. Heritability estimates for WAW1 was low and there is no other result in the literature for comparison of this trait.

### 3.4. Direct and correlated responses

Direct and correlated responses to selection for TFW on fibre traits over the 8 years of selection are presented in Fig. 2. In the low line, mean breeding value of TFW per cohort of animals born the same year decreased sharply from 1995 to 1997, was stable between 1997 and 1999 and then decreased again. On the contrary, in the high line, mean breeding value for TFW increased estimated from multivariate analysis using 9LW as a covariate. The heritability estimate for 9LW was high and in agreement with previous results (Allain et al., 1996, 1999). In Chinese angora rabbits, Lin et al. (1995) reported a heritability estimate of 0.43 for live weight. Caro et al. (1984) reported a high genetic correlation (0.70) between body weight and wool production at third shearing in the German breed. Rochambeau (1988) observed a positive relationship between fleece weight and live body weight only in the first harvest with a significant phenotypic correlation. Thébault et al. (1992) also showed that fleece weight increases with body weight up to 4 kg. In our study, phenotypic and genetic correlation estimates between TFW and body weights were not significantly different from zero, except between TFW and 9LW, where a low genetic correlation estimate (0.26) was observed.

### Table 5

<table>
<thead>
<tr>
<th>Trait</th>
<th>$h^2$ TFW</th>
<th>$h^2$ Trait 2</th>
<th>$r_g$</th>
<th>$r_p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>LW4</td>
<td>0.35±0.05</td>
<td>0.30±0.04</td>
<td>-0.04±0.17</td>
<td>0.04±0.04</td>
</tr>
<tr>
<td>LW8</td>
<td>0.35±0.05</td>
<td>0.09±0.08</td>
<td>-0.12±0.28</td>
<td>0.06±0.04</td>
</tr>
<tr>
<td>LW12</td>
<td>0.35±0.05</td>
<td>0.14±0.09</td>
<td>-0.02±0.23</td>
<td>0.07±0.04</td>
</tr>
<tr>
<td>LW16</td>
<td>0.35±0.05</td>
<td>0.32±0.10</td>
<td>0.10±0.17</td>
<td>0.06±0.04</td>
</tr>
<tr>
<td>LW20</td>
<td>0.35±0.05</td>
<td>0.39±0.10</td>
<td>0.09±0.16</td>
<td>0.07±0.04</td>
</tr>
<tr>
<td>9LW</td>
<td>0.35±0.05</td>
<td>0.45±0.06</td>
<td>0.26±0.12</td>
<td>0.34±0.03</td>
</tr>
</tbody>
</table>

$r_g$: genetic correlation; $r_p$: phenotypic correlation.

Fig. 2. Change of mean breeding value estimates (EBV) of total fleece weight (TFW), bristly wool (WAJ1), woolly wool (WAW1) and homogeneity (HOM), over the 8 years of selection for both the high (▲) and low (■) lines. Genetic standard deviation ($\sigma_G$) is given for each trait.
sharply until 1995 and then slightly up to 2001. Substantial response was achieved through selection for TFW, with a divergence between the high and low lines in the mean breeding value of 80.95 g or 3.04 genetic standard deviations after 8 years of selection. Significant correlated responses to selection on TFW were also observed on other fibre traits and a divergence of 2.96, 2.78 and 1.21 genetic standard deviations were obtained for WAJ1, WAW1 and HOM, respectively. Thus a selection for TFW, a simple and easy criterion to measure, is very efficient to improve WAJ1 which is an important economical trait in French angora wool production.

Correlated response to selection for TFW on 9LW is shown in Fig. 3. In the initial cohort, a difference in mean breeding value estimates of 9LW was observed between the two lines in favour of the low line. Such a difference cannot be explained and could be due to a random sampling effect when the divergent selection experiment was initiated. After 8 years of selection for TFW, the difference in the mean breeding value of 9LW between the two lines decreased over years and was close to null at the end of the experiment. This result indicates that, as expected in regard to genetic parameters, an increase in live body weight was obtained by selection for total fleece weight.

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In the literature, there are no results about selection experiments for wool traits in the Angora rabbit. In other species, nearly all of the existing divergent selection studies in livestock science have been done on sheep. Bray et al. (2005) with a divergent selection experiment for wool growth rate, showed that sheep selected for high estimated breeding value produced more wool per day than sheep selected for low breeding value (on average 32.5 versus 17.7 g/day clean wool, respectively; \( P < 0.05 \)). Responses to selection for yearling fleece weight and live weight were studied in the Romney sheep on two selection lines, one selected for fleece weight and the other for live weight, and a control line (Johnson et al., 1995). Direct responses to selection, derived from deviations from the control line, were 1.20 kg and 11.9 kg for fleece weight and live weight respectively, \( i.e. \) about 2.5 phenotypic standard deviation for both traits. In sheep, as in angora rabbits in the present study, important genetic progress could be made by selecting for wool traits.

4. Conclusion

Selection for high and low total fleece weight was successfully performed in Angora rabbits and a divergence of three genetic standard deviations was observed between the high and low lines after 8 years of selection. Selection for TFW significantly increased WAJ1 which resulted from the highly positive genetic correlation between TFW and WAJ1. It is important to note that selection for easily measurable total fleece weight has a general beneficial effect on fleece quality. These genetically diverse lines are suitable for subsequent detailed studies of biological and physiological changes of the different fleece components brought about by selection on total fleece weight. A high quality fleece having a good ability to produce a fluffy yarn was characterised by a high weight of quality WAJ1 and high fleece homogeneity. All these characteristics were observed on the high line indicating that selection for total fleece weight results in an improvement of the quality of the fleece.

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