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Genetic control of resistance to gastro-intestinal parasites in crossbred cashmere-producing goats: responses to selection, genetic parameters and relationships with production traits

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Abstract

This paper investigates the genetic control of the resistance of goats to nematode parasites, and relationships between resistance and production traits. The data set comprised faecal egg counts (FECs) measured on 830 naturally challenged (predominant species *Teladorsagia circumcincta*), crossbred cashmere-producing goats over 5 years (1993-1997) and production traits (fibre traits and live weight) on 3100 goats from the same population in Scotland, over 11 years (1987-1997). Egg counts comprised repeated measurements (4 to 11) taken at 12 to 18 months of age and production traits, i.e. live weight and fibre traits, were measured at approximately 5 months of age. The goats for which FECs were available were subdivided into a line selected for decreased FECs, using the geometric mean FEC across the measurement period and goats not selected on the basis of FECs, acting as controls. The selected line had significantly lower FECs, compared with the control, in 4 out of 5 years (back transformed average proportional difference of 0.23). The heritability of a single FEC measurement (after cubic root transformation) was 0.17 and the heritability of the mean FEC was 0.32. The heritabilities of the fibre traits were moderate to high with the majority in excess of 0.5. The heritability of live weight was 0.22. Genetic correlations between FECs and production traits were slightly positive but not significantly different from zero. Phenotypic and environmental correlations were very close to zero with the environmental correlations always being negative. It is concluded that selection for reduced FEC is possible for goats. Benefits of such selection will be seen when animals are kept for more than 1 year of productive life.

Keywords: cashmere, genetic parameters, goats, nematoda, selection.

Introduction

Goats and sheep are normally managed under conditions which expose them to gastro-intestinal parasites, often leading to chronic subclinical infection and to loss of production of the host. Growth rate in lambs has been estimated to be reduced by up to, or even in excess of 25% in UK conditions (Coop *et al.*, 1985), where *Teladorsagia circumcincta* is the predominant parasite species.

Parasite control is normally achieved by a combination of anthelmintic treatment and pasture management. However, in recent decades there has

been increasing concern about the development of anthelmintic resistance in parasite populations (Jackson and Coop, 2000). It has been demonstrated that parasites harboured by goats develop resistance more quickly to anthelmintics than parasites harboured by sheep (Jackson and Coop, 2000). Control strategies, which are complementary to the use of anthelmintics and grazing management, are sought. Selection of sheep and goats for enhanced resistance to nematode infections is such an option.

Growing evidence now suggests that there is considerable variation between individual sheep in resistance to nematode parasites, as assessed by

faecal egg count (FEC), with heritabilities for FEC typically between 0.2–0.3 (Raadsma *et al.*, 1997; Morris, 1998). These heritabilities suggest that selection for resistance is feasible, and successful selection has been demonstrated in long-term experiments in New Zealand and Australia (Windon, 1990; Woolaston and Piper, 1996; Morris *et al.*, 1997a and 2000).

There have been fewer studies on goats than sheep and current knowledge is not as comprehensive. There is evidence that goats are more susceptible than sheep to gastro-intestinal nematode parasites (Le Jambre, 1984; Pomroy *et al.*, 1986; Huntley *et al.*, 1995). Therefore, it might be expected that the reduction in productivity and financial losses would be higher in goats than in sheep. However, compared with sheep, the heritabilities for FEC in goats are typically low (R. L. Baker, personal communication; Woolaston *et al.*, 1992; Morris *et al.*, 1997b; Mandonnet *et al.*, 2001).

Effective inclusion of resistance to gastro-intestinal parasites should be beneficial — improving resistance will help to alleviate concerns over treatment strategies and may also help to improve productivity. However, effective inclusion of resistance traits into breeding schemes requires knowledge of the genetic relationships between resistance and productivity. These relationships in sheep are currently contentious, because no clear pattern has emerged from research undertaken on Scottish Blackface sheep under upland conditions, Australian Merinos or New Zealand dual-purpose sheep. For goats there have been fewer studies and therefore the information available is much more limited. As goats are more susceptible to parasites and the parasites harboured by goats develop resistance to anthelmintics more quickly than the parasites harboured by sheep, the option of selecting goats resistant to gastro-intestinal parasites needs to be explored and estimates of the heritability of resistance and the relationship between resistance and production traits need to be investigated.

To investigate the potential of breeding cashmere-producing goats for resistance to gastro-intestinal nematode parasites, a study was initiated in Scotland in 1993 in which goats were selected for increased resistance, using FEC as the indicator trait. The study was prompted by the development of multiple anthelmintic resistance in the herd (Jackson *et al.*, 1992). The aims of this paper are threefold: firstly to estimate responses to selection for higher levels of resistance to gastro-intestinal parasites, secondly to estimate genetic and phenotypic parameters for faecal egg counts and thirdly to estimate correlations

with production traits. The production traits considered were live weight and traits related to fibre production and quality.

Material and methods

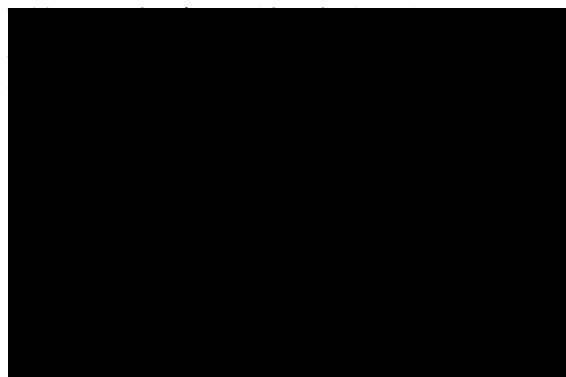
Goat population

The population studied has been described previously by Bishop and Russel (1994 and 1996). The goats were derived from Scottish feral goats and the importation of animals, embryos and semen from Iceland, Tasmania, New Zealand and the Gorno Altai region of Siberia between 1986 and 1988. A crossbreeding programme amongst the strains of goats produced a variety of purebred, two- and three-way crosses, distributed across a total of 18 commercial farms, including the Macaulay Land Use Research Institute's Sourhope Research Station, which served as a nucleus herd. The does gave birth to their first kids when they were approximately two years of age and were retained for 3 to 5 parities. The number of kids evaluated each year for production traits (see below) and included in the dataset is shown in Table 1, as are the number of sires and dams contributing to this dataset. From 1992 onwards only kids born in the nucleus herd were evaluated.

Selection as described below, was initiated for fibre traits in 1991 and nematode resistance in 1992. The nucleus was initially divided into three lines: a line selected on an index to improve the value of cashmere produced (190 does), a line selected for decreased fibre diameter (95 does) and an unselected control line (70 does). In 1992 another line was created, selected for resistance to gastrointestinal nematodes (helminth line, 95 does).

Parasitological measurements and selection procedure

The measurement criterion to assess the degree of parasite infection was FEC, i.e. the number of parasite eggs per gram of faeces. The method used



for determining FEC was a saturated salt flotation technique, modified from the method described by Christie and Jackson (1982). Apart from the initial screening described below, faecal egg counts were measured on goats of both sexes during their second grazing season when they were 12 to 18 months old, as previous experimental evidence suggested that kids in their first grazing season showed little resistance to parasites, and received suppressive anthelmintic treatment. The number of FEC measurements taken from an individual varied between years, from four to eleven.

One hundred mixed-age, adult male goats, from several herds were used in an initial screening in 1992 in which they were exposed to both artificial and natural *T. circumcincta* challenge. At the end of the challenge the two males with the lowest geometric mean FEC were bred with 95 unselected does to create the helminth line. The following year the same two males plus an additional two males with low FEC were used as sires (Jackson *et al.*, 1995). In subsequent years three males were selected each year from within the selection line, again using the geometric mean FEC as the selection criterion. To reduce potential inbreeding, selection was practised within family, i.e. the cohort of selected bucks each year did not include full- or half-sibs. Female replacements were chosen at random.

Responses in the helminth line were compared with goats that were unselected for nematode parasite resistance (control line). These goats generally corresponded to the goats used as the control for the fibre lines, but some additional goats from the 'value' and 'fine' lines were included to increase numbers. Selection line and control goats of the same sex were grazed together and thus faced the same parasite challenge. Additionally in 1996 a single FEC measurement was collected from all yearling goats on the farm not participating in the selection line *v.* control comparison. The structure of the population with parasitological measurements is given in Table 2.

The male yearlings were treated with anthelmintic at each sampling time for the first 2 years, but from year 3 were only treated at turn-out onto pasture in spring following an exposure to artificial challenge during winter housing. The female yearlings were always challenged during winter housing and then treated at turn-out on to pasture, and thereafter treated on each sampling occasion. Goats in this study seldom showed clinical signs of nematode infection. FEC from the artificial challenges are not included in this paper.

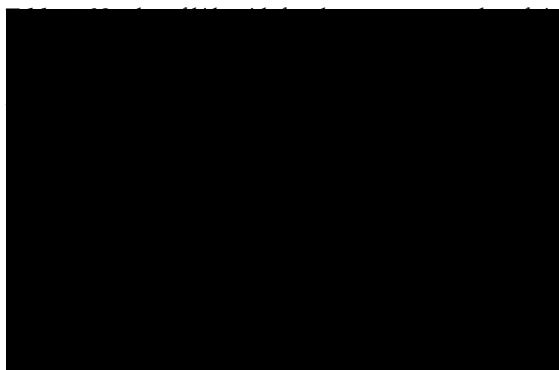
Production traits

Kids were evaluated for fibre characteristics on the basis of a 10-cm² mid-side patch of fleece sample taken at about 5 months of age. The sampling site was over the last rib half way up the side of the animal, as this site is considered to be representative of the fleece as a whole (Pattie *et al.*, 1989). Each year kids were sampled and recorded from all available lines.

The traits measured were as follows: live weight at 5 months of age (LW), cashmere weight in the 10-cm² patch sample (P_Cash), mean cashmere fibre diameter (Diam) and the standard deviation of fibre diameters in each sample (Diam_sd) and cashmere yield (Yield). Yield is cashmere weight as a proportion of total fibre weight. Until 1996, fibre diameter was measured following manual separation and weighing of guard hair and cashmere fibres, by projection microscopy using standard procedures (International Wool Textile Organisation (IWTO), 1989). In 1997, fibre diameter was determined by optical fibre diameter analyser (OFDA) according to specification IWTO-47-95 (IWTO, 1995). In the first 2 years of the trial, fibre length was measured directly on the animal at the time of sampling, however this measurement was subsequently discontinued. From 1992 onwards, staple length was measured on the laboratory samples, and for the purpose of analyses this is treated as the same trait as fibre length. Live weight was also recorded at the time of fibre sampling.

Data analysis

Distributions. The FEC measurements and cashmere traits were generally not normally distributed. It has been reported many times that FEC measurements often fit the negative binomial distribution. This distribution describes traits which show overdispersion in comparison with the normal distribution, with a small number of animals contributing a large proportion of the larvae to the



pasture (Barger, 1985; Stear *et al.*, 1995 and 1998). For example, in New Zealand studies it has been estimated that the most susceptible 10% of animals contribute 50% of the pasture contamination (McEwan, 1994). In this dataset the negative binomial distribution was fitted to the faecal egg count dataset within year, sex and line using the GENSTAT package (Lawes Agricultural Trust (LAT), 1993).

Two methods were used to identify the best transformation that would render faecal egg counts approximately normally distributed. In the first method, commonly used transformations (natural logarithm, square and cubic root) were made to the trait and they were tested for normality using the GENSTAT package (LAT, 1993). This algorithm uses a χ^2 test of association for testing the goodness of fit of the data to the defined distribution. The second method was a Box-Cox transformation using the equation given by Sokal and Rohlf (1995). The objective of this method is to find the best transformation for a given dataset (Y). This is done by estimating $Y' = (Y^\lambda - 1)/\lambda$, for $\lambda \neq 0$, and $Y' = \ln Y$, for $\lambda = 0$. A log likelihood is then estimated as $L = -v/2 \ln s^2 + (\lambda - 1)v/n \sum \ln y$, where, v are degrees of freedom from analysis of variance and s^2 is the error mean square based on n degrees of freedom. The value of λ which maximizes the log-likelihood function yields the best transformation to normality. The best transformation (from both methods) was found to be the cubic root (see **Results** section).

Statistical model specification. Least-squares analysis of variance was undertaken in order to identify important sources of variation. Fixed effects which were fitted included year, farm, date of birth, sex, if the animal was born to its genetic mother or by MOET (multiple ovulation and embryo transfer) procedure (practised to spread genotypes across farms during the initial expansion of the population) and litter size. The genetic origin of the animals i.e. proportion of different genotypes, was also fitted. For the FECs the proportion of Icelandic genotype was the only genetic group effect found to be significant and it was fitted as a covariate [regression coefficient ($\sqrt[3]{\text{FEC}} = 1.70$ (s.e. 0.49) \times proportion (Icelandic)]. All the significant first degree interactions were fitted as well.

The same fixed effects described above were used for analyses of production traits, and the same procedure for finding the appropriate model was performed. For the fibre diameter a code for the operator who performed the measurement was also available and fitted as a fixed effect.

The fixed effects which were found to be significant were fitted in a REML analysis performed in GENSTAT (LAT, 1993), fitting also sire as a random effect. For each year the mean FEC of the selected line and control animals were compared using a t test.

Genetic parameter estimation. An animal model was fitted, using ASREML (Gilmour *et al.*, 1996), for estimating the additive genetic variance components for both the FEC measurements and the production traits, using all known pedigree relationships. For faecal egg counts ($\sqrt[3]{\text{FEC}}$), permanent environmental effects, i.e. the environment covariance between the repeated observations on the same animal, and genetic maternal effects were fitted in turn. The likelihood ratio test was used to distinguish between models and select the most parsimonious model.

The genetic origin of the goat has a large effect on all production traits (Bishop and Russel, 1994 and 1996). It was accounted for by regressing the measurement for each kid on the proportion of each of the five strains which comprised its own genotype. This assumes no heterosis effects, which is a reasonable assumption for the fibre traits (Bishop and Russel, 1994). The resulting heritabilities may be thought of as within-strain heritabilities. For FEC, as described above, only the proportion of Icelandic genotype was fitted as a covariate.

Bivariate analyses of the production traits with FECs were performed using the mean of the FEC measurements for estimating genetic and phenotypic correlations between traits. All available production data were used to maximize the precision of the estimates. Phenotypic correlations for a single FEC measurement were estimated from the results, rescaling the environmental variance by the average number of measurements per animal.

Results

Summary of traits and their distribution

In Table 3 the mean, minimum and maximum values for each trait are shown along with the phenotypic standard deviations.

For FECs, the cubic root transformation proved better than the square root or the logarithmic transformation in making the data approximately normally distributed. Box-Cox transformation gave a λ value of 0.33 indicating that the cubic root was the best transformation for this particular dataset. It should be noted that the λ value is an empirical one, however there are particular values which point to commonly used transformations: 1 points to the linear, 0 to the logarithmic, 0.5 to the square root and 0.3 to the cubic root. For the production traits,

P_Cash was skewed and not normally distributed but a logarithmic transformation was used to create an approximately normally distributed trait.

The negative binomial distribution was fitted to the FEC measurements. This distribution is described by two parameters: m and k . Parameter m is the mean and k describes the aggregation of the distribution: as $k \rightarrow 0$ the majority of the parasite population is concentrated on fewer animals, and as $k \rightarrow \infty$ the parasite population is more randomly distributed (Anderson and May, 1992). As mentioned above, the GENSTAT statistical package tests the fit of the data to the specified distribution using a χ^2 test of association. The data fitted the negative binomial distribution in only 4 out of 20 year \times line \times sex cohorts.

Averaging across the whole data set, the parasite burden of the 5% of the animals with the highest FEC contributed 19% of the eggs dropped to the pasture and the parasite burden of the 10% animals with the highest FEC contributed 31%.

Selection responses of FEC

In Figure 1a the mean of the cubic-root-transformed faecal egg counts (CFEC) of both the control and the selected animals are given, along with the standard errors of the mean. The mean values are not shown for the pre-screening population of the sires as there is no valid comparison between those and subsequent values. Therefore, the results are given from the first generation of selected animals onwards. In Figure 1b the back-transformed means are shown for the cubic root transformation, for both lines.

Heritabilities of FEC

For FEC the models which included maternal genetic effects or permanent environmental effects were found to fit the data no better than the ones without them, using the likelihood ratio test. However, fitting the permanent environmental effects allowed estimation of the within-season repeatability of FEC.

In Table 4 heritabilities and repeatabilities and their standard errors are given for FEC, on the cubic root scale (CFEC) for a single FEC measurement. The heritability of the mean FEC for each animal was 0.32



(s.e. = 0.09). These parameters were estimated with the proportion of Icelandic genotype fitted as a covariate.

When the proportion of the Icelandic genotype was not fitted, the heritability on the cubic root scale increased, slightly, to 0.18 (s.e. 0.02) when permanent environmental effects were not fitted, but did not change when they were fitted (0.14, s.e. 0.03). There was a slight increase in repeatability when the proportion of Icelandic was not fitted (0.18, s.e. 0.02). When the mean of repeated measurements was taken the heritability on the cubic root scale increased to 0.39 (s.e. 0.08).

Heritabilities of production traits

Heritabilities with standard errors are given in Table 5 for the cashmere traits both on the logarithmic and observed scale. It should be noted that the heritabilities of live weight were estimated with a model that included maternal genetic effects. Fitting the covariance between direct genetic and genetic maternal effects did not improve the model and therefore the covariance of these effects was not included in the analysis. The maternal genetic effect for live weight, as a proportion of phenotypic variance, was estimated to be 0.28 (s.e. 0.03). When the maternal genetic effects were not included the heritability estimate was 0.50 (s.e. 0.05).

Correlations between FECs and production traits

In Table 6 the genetic, phenotypic and environmental correlations of production traits with the mean of several FEC measurements and with one measurement are shown. Standard errors are shown for genetic correlations. As can be seen all the correlations are small to moderate, and not significantly different from zero, although the genetic correlations are always more positive than the phenotypic and the environmental correlations. The environmental correlations are all slightly negative.

Discussion

The aim of this study has been to explore the possibility of breeding for resistance to gastro-intestinal parasites in goats. The indicator trait of resistance to gastro-intestinal parasites, FEC, was found to be heritable albeit less heritable than the same trait in sheep. The fibre related traits were found to be generally highly heritable traits. Live weight was the only trait for which maternal effects were found to be important and this trait was found to be moderately heritable. The genetic correlations between production traits and FEC were always positive, although not significantly different from zero, whereas the phenotypic and environmental correlations were clustered around zero.

Many previous experiments in sheep have shown that it is possible to breed for reduced FECs. The mean FEC of the control and the selected lines in this study were different in the first three years and there was a tendency in the last 2 years for the two lines to diverge further apart. The significant difference between the two lines in conjunction with the fact that FEC is a heritable trait shows that successful breeding for reduced FECs is possible in goats as it is in sheep.

The heritability of a single FEC measurement was found to be low compared to the majority of values published (usual range 0.2 to 0.4) for sheep. The



heritability of a single FEC measurement when permanent environmental effects were not fitted was found to be equal to the repeatability when permanent environmental effects were fitted. There are indications from this data set that the environmental correlation changes between different measurements. Measurements taken close together in time tend to have a positive correlation but the correlation reduces, even becoming negative, as the time between measurements increases. This observation and its consequences will be studied in this dataset in a subsequent analysis.

Previous studies have suggested that the heritability of FEC in goats is relatively low. Woolaston *et al.* (1992) estimated a heritability of 0.04 (s.e. 0.03) for weaners and 0.08 (s.e. 0.06) for adults. The experiment was conducted in Fiji and involved 1513 weaners (defined as <365 days old) and 789 adult goats (defined as >365 days old). The permanent environmental effect was 0.00 (0.11) which indicated that the repeatability is not greater than the heritability. Morris *et al.* (1997b) in a study of Saanen does in New Zealand estimated an overall heritability of FECs of 0.05 (s.e. 0.03). It must be noted that all the other studies have been performed in the tropics where *Haemonchus contortus* is the predominant species. The present study was performed in a temperate region (Scotland) where the predominant species is *T. circumcincta*.

Heritability estimates presented by Baker (1998) for goats under African conditions were 0.11 (s.e. 0.11) for weaners and 0.03 (s.e. 0.03) for kids at 6 months of age. Assuming that the same, or similar, immunological mechanisms act in both goats and sheep, and given the observation (Bishop *et al.*, 1996) that the expression of genetic control in sheep increases with age, the kids studied by Baker (1998) may have been too young for their defence mechanisms to be effective. In a subsequent analysis of the same data set Baker *et al.* (2001) estimated heritabilities of 0.08 (s.e. 0.07) at 2 months of age, 0.26 (s.e. 0.15) at 4.5 months of age and 0.08 (s.e. 0.12) at 14 months of age. The relatively large standard errors are due to the fact that comparatively small numbers of animals were measured.

Mandonnet *et al.* (2001), in a study in Guadeloupe in the French West Indies, estimated genetic parameters for resistance to worms in a population of Creole goats. Their estimate of heritability was 0.20 at 82 days of age. Post weaning, the estimate of heritability was 0.14 (s.e. 0.05) at 4 months of age and 0.33 (s.e. 0.06) at 10 months of age. It should be noted that the heritabilities at the 4 and 10 months of age were estimated for the mean of two measurements taken 1

week apart. Assuming that they represent the same infection these heritabilities are higher than the ones which would have been estimated on the basis of one measurement.

Naïve lambs start to mount an immune response, demonstrated by an increase in the heritability of the trait, when they come to be challenged by parasites. Faecal egg counts appear to become a heritable trait for lambs at approximately 3 months of age (Bishop *et al.*, 1996). Lloyd (1987) suggested information from sheep population studies could be used to extrapolate for goat populations. It could be suggested that goats develop an immunity response in a pattern similar to sheep. However, goats are more susceptible to parasites than sheep (Le Jambre, 1984; Pomroy *et al.*, 1986; Huntley *et al.*, 1995), although the reasons for this increased susceptibility are not known. It may be hypothesized that the feeding behaviour of goats (browsing), which would result in exposure to lower levels of larval intake than in sheep (grazing), has led this species to a different evolutionary pathway where resistance to parasites was (is) not an important trait because goats were (are) not exposed to such high levels of parasites as sheep. This increased susceptibility might also be accompanied by a late expression of immunity. Therefore goats might express a genetically influenced immune response at a later age than sheep (R. L. Baker, personal communication). The trend of the Baker *et al.* (2001) estimates is a for steady increase in heritability during the first 4.5 months of an animal's life, then a steady flat phase till 10 months of age and then an equally steady decrease till the 14 months of age (last data point). Given this observation it could be suggested that the increase in heritability is associated with a phase of acquisition of immunity, which may last longer in goats compared with sheep. As mentioned before the standard errors of the estimates of Baker *et al.* (2001) were large and the estimates themselves were not significantly different from each other.

As mentioned above, the heritability of the mean of several measurements is higher than that of a single measurement, as taking the mean of multiple measurements reduces the variance due to the reduction of non-permanent environmental effects. The amount by which it is reduced depends on the number of measurements taken and the repeatability. For a trait such as FECs for which the environmental conditions have a large effect there is, theoretically, a lot to be gained from multiple measurements (Falconer and Mackay, 1997). In the present study the number of measurements taken was approximately 7 in 1993 and 1995, 11 in 1994, 4 in 1996 (some animals

had one measurement in 1996), and 5 in 1997. The repeatability of FECs was found to be 0.17. As with all low heritability and low repeatability traits, more FEC measurements will result in an increase in the heritability of the trait and therefore an increase in the accuracy of the estimate of an individual animal's breeding value. In this particular case ($h^2 = 0.11$, $r_e = 0.17$, repeatability model), using quantitative genetics theory, it can be estimated that the heritability of the mean of three measurements will increase to 0.27 and that of five measurements to 0.36 approximately. In practice, the benefit of a more accurate estimation of an individual's breeding value should be weighed against the cost of the extra measurements.

Most of the heritabilities found for cashmere traits are high compared to the estimates for other production traits, and are in general agreement with previous studies (Bishop and Russel, 1996; Gifford *et al.*, 1990; Bigham *et al.*, 1993). Live weight was the only trait for which significant maternal effects were found. Fitting maternal effects resulted in a change in the heritability estimate from 0.50 to 0.22. The estimated heritability was similar to that of Gifford *et al.* (1990) and somewhat lower than that of Bishop and Russel (1996). As pointed out by Bishop and Russel (1994) live weight, unlike the fibre traits, showed heterosis. In this analysis it was assumed that there was no heterosis. The present dataset is larger than the one used by Bishop and Russel (1996), i.e. it is the same dataset augmented by several more years of data. Therefore there is much more information and a deeper pedigree, which is essential for estimating maternal effects. Therefore, the difference in the estimated heritabilities and maternal effects are probably due to the extra information available in this analysis.

The results of the bivariate analysis indicate that FECs and cashmere traits are phenotypically uncorrelated, although there are indications of small unfavourable genetic correlations. This is in agreement with most findings for sheep, where wool production traits have a small or zero correlation with FEC (Woolaston, 1990; Morris *et al.*, 1997a and 2000; Greef and Karlsson, 1999). Resistance to gastrointestinal parasites in kids, as results from studies have so far shown (R. L. Baker, personal communication; Mandonnet *et al.*, 2001), is not genetically correlated with live weight. Therefore, selection for resistance is unlikely to have a correlated genetic effect on live weight, although it might influence fibre traits decreasing both fibre weight and diameter. Economically, however these two effects on cashmere are in the opposite direction, and predicted responses in overall fleece value using

the cashmere production index, as described by Bishop and Russel (1994), are negligible. An environmental advantage of selection for reduced FECs will be lowered pasture contamination, with possible longer-term benefits in reduced parasite challenge, as described by Bishop and Stear (1997 and 1999).

The results of this study show that there is potential for breeding for reduced FECs, an indicator of resistance to gastro-intestinal parasites, in goats. It is important to note that with the currently available information, and if the hypotheses described above are true, it is more difficult to exploit the heritable variation in goats than in sheep, as they express genetic variation in resistance to gastro-intestinal nematode parasites at an older age. Breeding for resistance to worms is likely to be beneficial in cases where the animals are kept for more than one year of productive life, such as in the case of milk production or fibre production, assuming that genetic differences in resistance are expressed in adult animals. As in the case of sheep there will be a benefit of multiple measurements and a compromise should be made between cost and increased heritability. An aspect which needs to be addressed in studies investigating the genetic control of resistance in goats is the age at which the resistant animals express their superiority. Ward *et al.* (1999) has shown that resistant lambs begin to express resistance earlier than other lines. In goats where resistance is expressed at comparatively late ages, this is of considerable importance.

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