Genetic parameters for fecal egg counts and their relationship with body weights in Katahdin lambs

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ABSTRACT: Reliance on anthelmintic drugs to control internal parasites in sheep is no longer sustainable because of the development of resistance to these drugs in parasite populations. Genetic selection may offer an alternative long-term solution, as differences in parasite resistance exist both within and among sheep breeds. However, selection for parasite resistance may have correlated effects on other production traits. The objectives of this study were to estimate genetic parameters for weaning (**WFEC**) and postweaning (**PWFEC**) fecal egg counts (**FEC**) and assess their relationship with birth (**BWT**), weaning (**WWT**), and postweaning (**PWWT**) BW in Katahdin lambs. The study used WFEC ($n = 2,537$), PWFEC ($n = 3.421$), BWT ($n = 12,869$), WWT ($n = 10,961$), and PWWT ($n = 7,812$) from 12,869 lambs measured between 2003 and 2015 in 13 flocks enrolled in the U.S. National Sheep Improvement Program. Animal and sire models were fitted to the data using the ASReml statistical package. Records were corrected for fixed effects of dam age, joint effect of type of birth and rearing, and management group (defined by joint effects of flock, sex, and birth year and season); lamb age in days at each measurement time was fitted as a covariate. Maternal additive and maternal permanent environmental effects were not significant ($P > 0.05$), but litter effects influenced ($P < 0.01$) both WFEC and PWFEC. Heritability estimates ranged from 0.18 to 0.26 for WFEC and 0.23 to 0.46 for PWFEC, depending on the model used. Heritability estimates from sire models were higher than estimates from animal models. Direct additive, litter, residual, and phenotypic correlations between WFEC and PWFEC were 0.82, 0.25, 0.15, and 0.29, respectively. Bivariate analyses revealed low to moderate correlations between BW and FEC. Moderate heritabilities for FEC in this study indicated that genetic progress for this trait can be achieved in Katahdin lambs and that selection for low FEC should have little or no effect on BW.

Key words: body weights, fecal egg count, genetic correlations, Katahdin sheep

INTRODUCTION

Gastrointestinal nematode (**GIN**) parasites are a worldwide problem for the sheep industry, causing reduced production and economic losses. In addition, increases in the incidence of resistance of parasites to anthelmintic drugs (Howell et al., 2008; Kaplan and Vidyashankar, 2012; Leathwick and Besier, 2014) limit the efficacy of pharmacological control of GIN. The fecal egg counts (**FEC**) are measured as the number of eggs per gram of feces (**epg**) and is the most common indicator of parasite infection. Variation in parasite resistance exists within and among sheep breeds (Courtney et al., 1985; Vanimisetti et al., 2004a,b; Karlsson and Greeff, 2012; Brown and Fogarty, 2017), indicating that selection can be used to reduce FEC. Genetic selection for parasite resistance results in permanent genetic change that is expressed throughout the animal's life (Bishop, 2012). However, selection for low FEC may influence other economic traits. Estimation of correlations between parasite resistance and other traits is therefore necessary for the development of breeding programs. If selection for parasite resistance does not negatively affect other traits, positive outcomes are expected for both animal health and the economic efficiency of production (Nieuwhof and Bishop, 2005). Heritability estimates for FEC appear in the literature for several sheep breeds (Bisset et al., 1992; Vanimisetti et al., 2004a; Safari et al., 2005; Assenza et al., 2014; Brown and Fogarty, 2017), but information on the Katahdin breed is limited (Notter, 2013). The Katahdin is a composite breed of sheep developed in Maine, USA, beginning in the 1950s by crossing hair and wool breeds (Wildeus, 1997). Several studies have reported parasite resistance or resilience in Katahdin sheep (Burke and Miller, 2002, 2004; Vanimisetti et al., 2004b), and EBV for FEC have been available to Katahdin breeders that participate in the U.S. National Sheep Improvement Program (**NSIP**; www.nsip.org) since 2007. Objectives of this study were to estimate genetic parameters for weaning (**WFEC**) and postweaning (**PWFEC**) FEC and their correlations with birth (**BWT**), weaning (**WWT**), and postweaning (**PWWT**) BW in Katahdin lambs.

MATERIALS AND METHODS

Data

This study used data on 12,869 lambs born between 2003 and 2015 to 314 sires and 2,849 dams in 13 NSIP Katahdin flocks located in the eastern United States between 31.0 and 40.8 North latitude and between −74.0 and −93.9 West longitude. All flocks were located in areas considered vulnerable to parasitism with *Haemonchus contortus*. Fecal samples at approximately 60 (weaning) and (or) 120 d of age (postweaning) were available for 4,676 lambs. Fecal samples were collected directly from the rectum, and FEC were determined using a modified McMaster technique (Whitlock, 1948), with a sensitivity of 25 or 50 epg, depending on the laboratory. Records from single, twin, triplet, and quadruplet lambs (n = 2,401, 7,682, 2,614, and 172, respectively), lambs raised in litters of 1, 2, or 3 (n = 2,727, 7,239, and 1,640, respectively) and with dams that were between 10 mo and 10 y (126 mo) old at lambing, were used for the study. Management groups with less than 5 records or with average FEC of less than 500 epg were also excluded from the analyses. The final data contained 2,537 WFEC; 3,421 PWFEC; 12,869 BWT; 10,961 WWT; and 7,812 PWWT records.

Statistical Analyses

Genetic parameters for FEC were estimated using the ASReml statistical package (Gilmour et al., 2015). The FEC were not normally distributed and were transformed as $\ln_{10}(\text{FEC} + 25)$ before analyses. Fixed effects of dam age in year (1 to 10), joint effect of type of birth and rearing, and management group (representing joint effects of flock, sex, and birth year and season) and a continuous effect of lamb age at measurement were included in all models.

A random direct additive effect was included in all models. The significance of additional maternal permanent environmental, maternal additive, and maternal temporary environmental (i.e., litter) effects was then tested sequentially using the following models:

$$\mathbf{Y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{e} \tag{1}$$

$$\mathbf{Y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_c c} + \mathbf{e} \tag{2}$$

$$\mathbf{Y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{e} \tag{3}$$

$$\mathbf{Y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{Z_c c} + \mathbf{e} \tag{4}$$

$$\mathbf{Y} = \mathbf{Xb} + \mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{Z_c c} + \mathbf{Z_l l} + \mathbf{e} \tag{5}$$

where **Y** is a vector of records for each trait; **b**, **a**, **m**, **c**, **l**, and **e** are vectors of fixed, random direct

additive, maternal additive, maternal permanent environmental, litter, and residual effects, respectively; and $\mathbf{X}$, $\mathbf{Z_a}$, $\mathbf{Z_m}$, $\mathbf{Z_c}$, and $\mathbf{Z_l}$ are corresponding incidence matrices.

Additional random effects in Models 2, 3, 4, and 5 were tested using log-likelihood ratio tests. A chi-square distribution with 1 df was used to determine significance levels for differences in likelihoods [$2(\text{LogL}_1 - \text{LogL}_0)$] between adjacent models. Convergence was assumed when changes in log likelihood in successive iterations were less than $0.002 \times$ the current iteration number. Phenotypic variance (σ^2_p) was estimated as the sum of the variance components; direct (h^2) and maternal (m^2) heritabilities were σ^2_a/σ^2_p and σ^2_m/σ^2_p, respectively; the permanent environmental effect (c^2) was σ^2_c/σ^2_p; and the litter effect (l^2) was σ^2_l/σ^2_p where σ^2_a, σ^2_m, σ^2_c, σ^2_l, and σ^2_p are direct additive, maternal additive, maternal permanent environmental, litter, and phenotypic variances, respectively.

Expression of genetic variation in parasite resistance is necessarily contingent on some minimum level of parasite challenge, which was the basis for excluding records from management groups with means for FEC of less than 500 epg in the main analysis. However, there is no objective basis for setting a necessary minimum level of parasite challenge for detection of genetic variation in parasite resistance. The minimum mean FEC of 500 epg is arbitrary. In addition, variation among flocks, years, and management groups in mean FEC raised concerns regarding the consistency of genetic parameters for FEC among management groups that differed widely in mean FEC. This issue was considered by subdividing the WFEC and PWFEC data sets into 3 Subsets (A, B, and C) with management group means for FEC of less than 500, 500 to 1,500, or greater than 1,500 epg. The value of 1,500 epg that was used to assign records to Subset B or C was chosen to place approximately equal numbers of records and management groups in the 2 subsets. For WFEC, Subset A contained 804 records from 75 management groups, Subset B contained 1,424 records from 72 management groups, and Subset C contained 1,201 records from 93 management groups. For PWFEC, Subset A contained 1,203 records from 142 management groups, Subset B contained 1,654 records from 127 management groups, and Subset C contained 1,949 records from 132 management groups. Genetic parameters were estimated for each subset using the best-fitting models for the combined data set.

Supplemental analyses were used to compare estimates of heritability for FEC between animal and sire models. Initial estimates of heritabilities for FEC used to derive NSIP EBV (Notter, 2013) were based mainly on variation among paternal half-sib families. However, the current data also included relatively large numbers of parent–offspring pairs with FEC records in different years and management groups (Table 1). Sire models were fitted by replacing $\mathbf{Z_a}\mathbf{a}$ with $\mathbf{Z_s}\mathbf{s}$, where $\mathbf{s}$ is a vector of additive sire effects and $\mathbf{Z_s}$ is an incidence matrix relating records to sires. The additive variance then was estimated as $4 \times$ the sire component of variance (σ^2_s), and heritability was estimated as ($4\sigma^2_s/\sigma^2_p$).

Table 1. Demographic summary for animals with weaning (WFEC) and postweaning (PWFEC) fecal egg counts

	Variable					
	WFEC			PWFEC		
	Number	Number of lambs		Number	Number of lambs	
Item	Number	Mean	Median	Number	Mean	Median
Number of records	2,537	–	–	3,421	–	–
Number of flocks	12	211.5	159.5	12	285.1	219.5
Number of management groups	122	20.8	17.0	166	20.6	16.0
Number of sires	144	17.4	13.0	187	18.0	11.0
Number of sires used in >1 flock[a]	10	–	–	17	–	–
Number of dams	1,103	2.29	2.0	1,429	2.39	2.0
Number of litters	1,626	1.55	1.0	2,281	1.49	1.0
Number (%) of dams with records[b]	209	–	–	439	–	–
Number (%) of sires with records[c]	35	–	–	53	–	–

[a]Six, 3, and 1 sires had progeny in 2, 3, and 4 flocks, respectively.

[b]For WFEC, these 209 dams represented 18.9% of all dams and produced 25.7% of measured lambs. For PWFEC, these 439 dams represented 30.7% of all dams and produced 32.0% of measured lambs.

[c]For WFEC, these 35 sires represented 24.3% of all sires and produced 24.8% of measured lambs. For PWFEC, these 53 sires represented 28.3% of all sires and produced 28.4% of measured lambs.

Correlations between WFEC and PWFEC and between FEC and BW were estimated using bivariate animal models. Bivariate models for WFEC and PWFEC included only significant random effects on FEC. Models for BW in bivariate analyses included the same fixed effects that were fitted for FEC, as well as random direct additive, maternal additive, maternal permanent environmental, litter, and residual effects (Ngere et al., 2017a).

RESULTS

Weaning FEC ranged from 0 to 44,000 epg, with an average of 851 epg, and PWFEC ranged from 0 to 87,000 epg, with an average of 794 epg. The CV, following logarithmic transformation, was 24% for both WFEC and PWFEC. Fixed effects of birth–rearing type and dam age were not significant ($P > 0.05$), but both WFEC and PWFEC differed ($P < 0.001$) among management groups. Regression coefficients describing the associations between transformed WFEC and PWFEC and lamb age were -0.002 ± 0.002 and -0.005 ± 0.001 per day, respectively, corresponding to expected declines in WFEC and PWFEC of approximately 0.2% and 0.5% per day, respectively.

Table 1 summarizes the distribution of FEC records among flocks and management groups and provides information about the genetic relationships that were present in the data. After excluding management groups with fewer than 5 observations or mean FEC of <500 epg, 1 flock had no remaining management groups for WFEC and 1 other flock had no remaining management groups for PWFEC. Mean numbers of records per management group and per sire

were 20.7 and 17.7, respectively. Median numbers of records were somewhat, but not strikingly, smaller than corresponding means. For WFEC, only 10 of 144 sires had progeny in >1 flock. Over 1,100 dams had progeny in the data, with an average of 1.54 litters and 2.35 recorded lambs per dam (Table 1). An average of 24.8% of dams and 26.3% of sires had FEC records. These dams and sires produced an average of 28.9% and 26.6%, respectively, of recorded lambs. Twenty-seven percent of the lambs had records for both WFEC and PWFEC.

Estimates of Genetic Parameters

Univariate models. Direct additive, maternal additive, dam permanent environmental, and litter effects were significant for all BW. Estimates of h^2, m^2, c^2, and l^2 were 0.15, 0.14, 0.06, and 0.16, respectively, for BWT; 0.16, 0.08, 0.04, and 0.19, respectively, for WWT; and 0.20, 0.06, 0.04, and 0.18, respectively, for PWWT.

For FEC, likelihood ratio tests based on animal models indicated that fitting dam permanent environmental or maternal additive effects in Models 2 and 3 did not improve goodness of fit for either WFEC or PWFEC. For WFEC, estimates of permanent environmental effect (c^2) in Model 2 and maternal heritability in Model 3 were both 0.01. Corresponding estimates for PWFEC converged to a value that was slightly outside the parameter space (-0.004 ± 0.010) for both effects. However, litter effects in Model 5 were significant for both FEC. Estimates of variance components for FEC from animal models that included only random direct additive, litter, and residual effects (Table 2)

Table 2. Estimates of variance components, variance component ratios, and SE from animal and sire models for weaning (WFEC) and postweaning (PWFEC) fecal egg counts for Katahdin lambs

	Animal models			Sire models	
Item[a]	WFEC	PWFEC	Item[b]	WFEC	PWFEC
σ^2_a	0.06 ± 0.02	0.09 ± 0.02	σ^2_s	0.02 ± 0.01	0.04 ± 0.01
σ^2_l	0.05 ± 0.01	0.04 ± 0.01	σ^2_l	0.07 ± 0.01	0.04 ± 0.01
σ^2_e	0.23 ± 0.02	0.25 ± 0.01	σ^2_e	0.26 ± 0.01	0.29 ± 0.01
σ^2_p	0.35 ± 0.01	0.37 ± 0.01	σ^2_p	0.35 ± 0.01	0.37 ± 0.01
h^2	0.18 ± 0.05	0.23 ± 0.04	h^2	0.26 ± 0.08	0.46 ± 0.08
l^2	0.15 ± 0.03	0.10 ± 0.03	l^2	0.14	0.00
t_{fs}	0.23	0.23	t_{fs}	0.27	0.23

[a]For animal models, σ^2_a = direct additive variance; σ^2_l = variance due to litter effects; σ^2_e = residual variance; σ^2_p = phenotypic variance = $\sigma^2_a + \sigma^2_l + \sigma^2_e$; h^2 = heritability = σ^2_a/σ^2_p; $l^2 = \sigma^2_l/\sigma^2_p$; and t_{fs} = the full-sib correlation = $(0.5\sigma^2_a + \sigma^2_l)/\sigma^2_p$. The SE of t_{fs} was not available.

[b]For sire models, σ^2_s = direct additive variance among sires; σ^2_l = variance due to litter effects and included the direct additive variance among dams; σ^2_e = residual variance and included the Mendelian sampling variance for direct additive effects; and σ^2_p = phenotypic variance was estimated as $\sigma^2_s + \sigma^2_l + \sigma^2_e$. For comparability with estimates derived from animal models, h^2 was estimated as $4\sigma^2_s/\sigma^2_p$, l^2 was estimated as $(\sigma^2_l - \sigma^2_s)/\sigma^2_p$, and t_{fs} was estimated as $(\frac{1}{2}h^2 + l^2)$. The SE of t_{fs} and l^2 were not available for sire models.

indicated that estimates of direct heritabilities were modest and somewhat smaller for WFEC (0.18) than for PWFEC (0.23). However, litter effects accounted for a larger proportion of phenotypic variance for WFEC (0.15) than for PWFEC (0.10). Estimates of full-sib correlations were moderate and the same (0.23) for WFEC and PWFEC.

Heritability estimates for WFEC and PWFEC from sire models (Table 2) were estimated as $(4\sigma^2_s/\sigma^2_p)$ and were 44% and 100% larger, respectively, than estimates from animal models. The estimated variance among litters from sire models included the direct additive variance among dams, and estimates of l^2 for sire models in Table 2 were therefore adjusted as $(\sigma^2_l - \sigma^2_s)\sigma^2_p$ assuming equality between direct additive sire and dam variances. After adjustment, estimates of l^2 for WFEC were similar for animal and sire models, but the estimate of l^2 for PWFEC was 0.00 for a sire model. Full-sib correlations for sire models were estimated as $\frac{1}{2}h^2 + l^2$ and were similar to estimates from animal models.

Estimates of variance components and their ratios for WFEC and PWFEC from animal models for 3 subsets of the data with different management group means are reported in Table 3. Lambs with management group means of less than 500 epg were not used in the analyses summarized in Table 2 and, for WFEC, estimates of additive genetic variance and heritability for these lambs did not exceed their SE. The 2 subsets of lambs with management group means for WFEC of greater than 500 epg appeared

Table 3. Effect of the average fecal egg count (FEC) of the management group on estimates of variance components and variance component ratios and their SE from animal models for weaning (WFEC) and postweaning (PWFEC) fecal egg counts

| Variable | Item[a] | Management groups with mean FEC of | | |
		<500	500 to 1,500	>1,500
WFEC	σ^2_a	0.02 ± 0.02	0.08 ± 0.03	0.07 ± 0.03
	σ^2_l	0.03 ± 0.02	0.06 ± 0.02	0.05 ± 0.02
	σ^2_e	0.21 ± 0.02	0.19 ± 0.02	0.26 ± 0.03
	σ^2_p	0.26 ± 0.01	0.33 ± 0.01	0.38 ± 0.02
	h^2	0.09 ± 0.09	0.25 ± 0.08	0.18 ± 0.08
	l^2	0.13 ± 0.08	0.18 ± 0.05	0.13 ± 0.05
PWFEC	σ^2_a	0.05 ± 0.02	0.08 ± 0.02	0.10 ± 0.03
	σ^2_l	0	0.05 ± 0.02	0.01 ± 0.02
	σ^2_e	0.14 ± 0.01	0.24 ± 0.02	0.26 ± 0.02
	σ^2_p	0.18 ± 0.01	0.37 ± 0.01	0.37 ± 0.01
	h^2	0.25 ± 0.08	0.21 ± 0.06	0.27 ± 0.07
	l^2	0	0.13 ± 0.05	0.03 ± 0.04

[a]σ^2_a = direct additive variance; σ^2_l = variance due to litter effects; σ^2_e = residual variance; σ^2_p = phenotypic variance = $\sigma^2_a + \sigma^2_l + \sigma^2_e$; h^2 = heritability = σ^2_a/σ^2_p; l^2 = σ^2_l/σ^2_p.

to have higher levels of additive genetic variation than lambs in the low-WFEC group, but did not differ greatly from one another. For PWFEC, all variance component estimates were smaller for the low-PWFEC group than for the other 2 groups. However, the heritability estimate for PWFEC in the low-PWFEC group was moderate in size and equal to 3.1 × its SE. Results in Table 3 suggested that measurable additive variation in PWFEC was present in all 3 subsets of the data but with much lower levels of variation for the low-PWFEC group. Bivariate models. The genetic correlation between WFEC and PWFEC (Table 4) was large and positive (0.82 ± 0.13). Litter, residual, and phenotypic correlations between WFEC and PWFEC were 0.25 ± 0.21, 0.15 ± 0.04, and 0.29 ± 0.02, respectively. Estimates of correlation coefficients among BW were also consistently large and positive (Ngere et al., 2017a).

For the 30 estimates of correlations between measurements of BW and FEC in Table 4, only 1 (−0.34 ± 0.15 between litter effects on PWWT and PWFEC) had an absolute value that both exceeded 0.10 and was larger than 2 times its SE. None had an absolute value that exceeded 0.40, suggesting no major antagonisms between lamb BW and FEC in these flocks. A few significant, but small, phenotypic correlations were present between BW and FEC, including favorable phenotypic associations between WFEC and both WWT (−0.07) and PWWT (−0.10) and an antagonistic phenotypic association of 0.07 between BWT and PWFEC.

An additional 7 correlations in Table 4 both exceeded 0.10 and exceeded their SE, suggesting need for further study of these relationships. These included favorable (negative) additive genetic correlations of WFEC with both WWT (−0.29 ± 0.19) and PWWT (−0.38 ± 0.21) and an antagonistic (positive) genetic correlation of 0.25 ± 0.14 between PWFEC and BWT. Antagonistic correlations were also present between additive effects on WFEC and PWFEC and future maternal additive effects on PWWT (0.21 ± 0.20 and 0.29 ± 0.15, respectively). Favorable correlations for litter effects between BWT and WFEC (−0.23 ± 0.13) and between WWT and PWFEC (−0.27 ± 0.15) suggested that positive effects on litter growth were associated with lower subsequent FEC.

DISCUSSION

Hair sheep breeds have been reported to be more resistant to parasite infection than wool breeds (Courtney et al., 1985; Zajac et al., 1990;

Table 4. Estimates of correlations and SE between weaning (WFEC) and postweaning (PWWEC) fecal egg counts (FEC) and between FEC and birth (BWT) weaning (WWT), and postweaning (PWWT) BW for Katahdin lambs[a]

Trait 1	Trait 2	r_d	r_l	r_e	$r_{a,m}$	r_p
WFEC	PWFEC	0.82 ± 0.13	0.25 ± 0.21	0.15 ± 0.04	n.e.[b]	0.29 ± 0.02
WFEC	BWT	0.10 ± 0.18	−0.23 ± 0.13	0.06 ± 0.05	−0.04 ± 0.17	0.01 ± 0.02
WFEC	WWT	−0.29 ± 0.19	0.05 ± 0.15	−0.06 ± 0.05	0.05 ± 0.19	−0.07 ± 0.03
WFEC	PWWT	−0.38 ± 0.21	0.09 ± 0.16	−0.10 ± 0.05	0.21 ± 0.20	−0.1 ± 0.03
PWFEC	BWT	0.25 ± 0.14	−0.002 ± 0.14	0.04 ± 0.04	−0.01 ± 0.13	0.07 ± 0.02
PWFEC	WWT	0.10 ± 0.16	−0.27 ± 0.15	0.01 ± 0.04	0.1 ± 0.15	−0.01 ± 0.02
PWFEC	PWWT	0.01 ± 0.17	−0.34 ± 0.15	−0.03 ± 0.04	0.29 ± 0.15	−0.02 ± 0.02

[a]r_d = additive genetic correlation; r_l = correlation between litter effects; r_e = residual correlation; $r_{a,m}$ = correlation between additive effects on FEC and maternal additive effects on BW; r_p = phenotypic correlation.

[b]n.e. = not estimated.

Burke and Miller, 2004; Vanimisetti et al., 2004b). The Katahdin, a composite breed developed from crosses between temperate wool and Caribbean hair breeds, has also been shown to have greater parasite resistance than wool breeds but to be less parasite resistant than Caribbean hair sheep breeds (Vanimisetti et al., 2004b; Palomo-Couoh et al., 2017). The NSIP Katahdin breeders measure FEC in lambs at weaning (between 45 and 90 d of age) and postweaning (usually between 90 and 150 d of age but occasionally up to 240 d of age) to assess variations in innate and acquired resistance to parasites (Notter, 2013). In general, older lambs with prior exposure to parasites are more resistant than younger lambs (Courtney et al., 1985).

Heritable phenotypic variation is necessary in order for genetic selection for parasite resistance to be successful. In our population, phenotypic CV following logarithmic transformation was moderate (24%) and the same for WFEC and PWFEC. Similar CV for Katahdin lambs (15% to 19%) but lower CV for Dorper (6% to 13%) and Dorset (7% to 12%) crossbred lambs was reported by Vanimisetti et al. (2004b). In a review of 16 independent estimates (Safari et al., 2005), the average CV for FEC was 30.7%. Phenotypic CV for untransformed FEC in Merino sheep was 45% to 47% but declined to approximately 30% after cube-root transformation (Brown and Fogarty, 2017). As also observed in this study, effects of birth/rearing type and dam age were not significant for FEC in artificially challenged Romney sheep (McEwan et al., 1992) or naturally infected Merino sheep (Pollott and Greeff, 2004a; Huisman et al., 2008).

Heritability estimates for FEC from this study indicated that improvement of FEC is possible through selection. Heritability estimates of 0.18 for WFEC and 0.23 for PWFEC from animal models were similar to the average heritability of FEC of 0.27 reported by Safari et al. (2005) and estimates of 0.19 to 0.26 in Merino sheep (Brown and Fogarty, 2017), 0.26 ± 0.01 in Romney sheep (Morris et al., 2010), and 0.25 in Uruguayan Merino sheep (Goldberg et al., 2012). However, lower estimates of 0.10 in lambs of 50% Dorset, 25% Rambouillet, and 25% Finnsheep ancestry (Vanimisetti et al., 2004a) and 0.10 ± 0.03 in Dorper sheep (Ngere et al., 2017a) were also reported.

Heritability estimates for FEC from the current study were lower than estimates of 0.27 to 0.65 obtained in preliminary studies of NSIP Katahdin lambs (Notter, 2013). Results from Notter (2013) were based on a more limited sample of flocks and years than those used in the current study and included results of a field study designed to compare FEC of progeny of Katahdin sires. Heritability estimates from sire models in the current study, however, were higher than estimates from animal models (Table 2), especially for PWFEC, and more similar to those obtained by Notter (2013). Heritability estimates derived from field data are dependent on the specific relationships present in the data and assumptions of the analytical model. Data used in the current study included relatively large numbers of parents and offspring with FEC (Table 1). Heritability estimates derived from resemblances between parents and offspring necessarily use records made in different years and management groups, and genotype × management group interaction would reduce resulting heritability estimates. Evidence for genotype × management group and genotype × location interaction was presented by Pollott and Greeff (2004b) and Li et al. (2011) in Australian Merino sheep. These interactions potentially reduced realized resemblances between parents and progeny but were expected to have a smaller effect on variation among half-sib families, especially when a majority of sires were used

in a single flock, as they were in both the current study and that of Notter (2013). Larger increases in heritability estimates between sire and animal models for PWFEC than WFEC suggested greater consistency in worm challenge among management groups for WFEC.

Greater estimates of h^2 from sire models could also arise if sires sampled by the flocks that contributed data to this study and, particularly, to the designed field study of Notter (2013) were not a random sample from the breed. Katahdin breeders that contributed to development of FEC EBV and subsequently practiced active selection for parasite resistance were particularly interested in identifying sires with high levels of parasite resistance and testing these sires against parasite-susceptible sires. Divergent selection of susceptible and resistant sires may have inflated the direct additive variance among sires and resulting sire component estimates of h^2. The present data do not allow definitive testing of this hypothesis, but convergence of the adjusted litter component of variance to zero and approximate equality of full-sib littermate correlations for animal and sire models suggest that dam and Mendelian sampling components of the direct additive variance may have been smaller than corresponding sire components. The current study documented the presence of significant additive variation in FEC in relatively young Katahdin lambs. Weaning FEC were collected at an average age of 68 d, with a 95% confidence interval of 45 to 91 d. By contrast, most previous estimates of genetic parameters for parasite resistance used measurements taken on older lambs. For example, weaning FEC in Australian Merino sheep were generally recorded at average ages of 90 to 100 d (e.g., Brown and Fogarty, 2017), and FEC records for Uruguayan Merino sheep were recorded at average ages of 9.5 and 11.6 mo (Ciappesoni et al., 2013). Active grazing and rumen development (to facilitate exsheathment and further development of L_3 larvae) by lambs rarely occurs before approximately 6 wk of age. With a prepatent period of 18 to 21 d for *H. contortus*, WFEC for a majority of the lambs in the current study were anticipated to have arisen from their primary parasite exposure and to reflect variation associated with innate immunity, though contingent on continued ingestion of infective larvae and the anticipated development of acquired immunity. By contrast, PWFEC were collected at an average age of 124 d, with a 95% confidence interval of 71 to 177 d and considered to reflect acquired immunity. A longitudinal study of FEC for *Teleodorsagia circumcinta*,

which is also an abomasal nematode parasite of sheep, in Scottish Blackface sheep yielded heritability estimates that were less than 0.01 at 4 and 8 wk of age, increased to 0.12 to 0.15 at 12 through 20 wk of age, and reached 0.22 at 24 wk of age (Bishop et al., 1996). These results suggested that there was no genetic variation in innate immunity to this parasite in this sheep breed. In a study of Merino sheep, Pollott et al. (2004) likewise reported an increase in heritability of FEC from 0.20 at weaning at an average age of 111 d to 0.65 at 400 d of age. Assenza et al. (2014) also obtained a higher estimate of heritability at a second controlled infection (0.48 to 0.55 at a mean age of approximately 133 d of age), compared with a first infection (0.21 to 0.38 at a mean age of approximately 100 d), in a backcross between Martinique Black Belly and Romane sheep. However, Brown and Fogarty (2017) obtained higher heritability estimates for FEC at weaning (0.29 ± 0.01) than at older ages (0.19 ± 0.01) in Merino sheep. Katahdin lambs thus appeared to exhibit genetic variation in innate resistance (or, perhaps, early acquisition of acquired immunity) to *H. contortus*. Variation in age-related changes in heritability estimates among lambs of different breeds, however, indicates that the optimal age for assessment of genetic variation in FEC must be based on data collected within the breed of interest.

In agreement with the current study, Pollott and Greeff (2004a) and Huisman et al. (2008) did not observe maternal effects on FEC in Merino lambs. A moderate effect of litter in our lambs was not surprising, however, with approximately 80% of lambs born in litters of 2 or more. Litter effects arise from temporary environmental effects common to litter mates. Despite the lack of evidence for multi-year maternal effects on lamb FEC in these data, litter effects may have included maternal additive and ewe maternal environmental effects that were unique to the litter and, perhaps, effects on parasite exposure associated with correlated grazing patterns for the ewe and her litter. Litter effects also include dominance genetic effects shared by full-sib lambs. Dominance effects have not been estimated for parasite resistance in sheep but may be important for advanced crosses between susceptible and resistant breeds.

Relatively little has been published about passive transfer of antibodies to gastrointestinal parasites and the impact of passive immunity on parasite susceptibility in lambs. Active grazing and associated initial exposure to gastrointestinal parasites seldom occurs before 6 wk of age

and corresponds to the waning of passive immunity. Bowdridge et al. (2013) compared levels of *H. contortus*-specific IgA in serum, colostrum, and milk of parasite-resistant St. Croix hair ewes and ewes of a parasite-susceptible wool-breed composite line. Ewes received a challenge dose of 10,000 larvae at the end of breeding and were then maintained in drylot during pregnancy. St. Croix ewes had higher levels of circulating parasite-specific IgA than composite ewes at lambing and at 3- and 6-wk postpartum. Parasite-specific IgA was present in colostrum and milk of ewes of both types, but levels of parasite-specific IgA in colostrum did not differ between breed types. These results thus did not reveal a mechanism for genetic differences (at a breed-type level) in passive immunity to *H. contortus* in young lambs.

Heritability estimates for PWFEC from animal models were relatively independent of management group means for FEC (Table 3), even for groups with means of <500 epg. By contrast, heritability estimates for WFEC for management groups with low-FEC means were lower than those for groups with higher mean FEC. Data used to estimate NSIP FEC EBV are currently restricted to management groups with mean FEC of >500 epg in order to ensure adequate parasite challenge to allow discrimination among individuals in parasite resistance. This restriction appears justified for WFEC but less important for PWFEC. Pollott and Greeff (2004b) used reaction-norm models and reported that heritabilities for FEC from sire models were higher in both high-FEC environments (>0.50) and low-FEC environments (up to 0.50) than in medium-FEC environments (approximately 0.25).

The high genetic correlation between WFEC and PWFEC in this population indicated that selection for low FEC in relatively young lambs would be effective in reducing FEC at later ages. Similar genetic correlations of 0.70 to 0.85 between FEC determined at different ages were reported for Romney sheep (Morris et al., 2010) and in preliminary analyses of NSIP Katahdin records (Notter, 2013). However, Brown and Fogarty (2017) reported lower genetic (0.40 ± 0.09) and phenotypic (0.07 ± 0.03) correlations between weaning and postweaning FEC for Merino sheep. Correlations between FEC and BW revealed little or no genetic antagonisms between these traits, in agreement with the review of Safari et al. (2005) and with results of Bisset et al. (1992) and Morris et al. (2010) in Romney sheep and Pollott and Greeff (2004a), and Brown and Fogarty (2017) in Merino sheep.

Estimates of (co)variance components for BW were reported and discussed by Ngere et al. (2017a). In the current study, a moderate and negative genetic correlation between WFEC and BW at weaning and postweaning was in the desired direction, suggesting that lambs with greater potential for postnatal growth also had lower WFEC. Negative, but smaller, associations were observed for residual and phenotypic correlations. A positive phenotypic association between BW and parasite resistance would not be surprising and would be expressed in our data as a negative association between BW and FEC. Such an association would potentially be self-reinforcing, with smaller lambs being more susceptible to parasitism and with greater levels of parasitism then further limiting subsequent growth. Negative associations between WFEC and BW at both direct additive and residual levels may have arisen from such a causal phenotypic association between BW and parasite susceptibility and would not necessarily be indicative of pleiotropic gene effects. Negative direct additive correlations between BW and FEC were observed only for WFEC, suggesting that favorable effects of BW on FEC may have been particularly important in young lambs where parasite resistance was anticipated to mainly reflect innate immune mechanisms. By contrast, PWFEC did not express consistent associations with postnatal BW, but both WFEC and PWFEC had positive direct additive associations with BWT. These associations suggest that expression of the acquired immune response was independent of or, at worst, slightly negatively associated with direct additive effects on BW.

Based on the direct-maternal correlations observed between FEC and BW, ewe lambs that had high WFEC and PWFEC tended to have subsequent favorable maternal effects on lamb weights. However, SE for these estimates were high. Notable among correlations between litter effects was that between PWFEC and PWWT, indicating that full-sib lambs that grew more rapidly than expected based on their predicted EBV also tended to have lower FEC.

In conclusion, evidence for additive genetic variation in both innate and acquired resistance to internal parasites was observed in this population of Katahdin sheep. Heritability estimates were moderate, and phenotypic CV was substantial for both weaning and postweaning FEC. A strong genetic correlation between WFEC and PWFEC indicated that selecting for one would result in improvement of the other. Relationships between FEC and BW revealed no important

genetic antagonisms between these traits. Breeding for increased resistance to internal parasites in Katahdin lambs would not be expected to have adverse effects on BW.

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