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The impact of sire fecal egg count estimated breeding values on indicators of offspring gastrointestinal nematode infection, and relative impact of lamb estimated breeding values on sale value of ram lambs

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ABSTRACT

Genetic selection of sheep for resistance to gastrointestinal nematodes (**GIN**) has become a priority for pasture-based production of lambs to minimize the need for deworming. The objective of this experiment was to determine the impact of sire weaning or post-weaning fecal egg count (**FEC**) estimated breeding value (**EBV**; WFEC and PFEC, respectively) from the National Sheep Improvement Program (**NSIP**) on GIN infection in Katahdin lambs born in fall (Oct – Nov; n = 459) or winter (Jan – Feb; n = 378) of 2018 through 2021 at the USDA Agricultural Research Service (**ARS**). FAMACHA scores were determined, and blood samples and feces were collected from the lambs to determine packed cell volume (**PCV**), and FEC at 60, 90, 120, and 150 days of age, and lambs were selectively dewormed if anemic. Data were analyzed using mixed models containing fixed effects of year, sex, age at sampling (fitted as a repeated measure), and their interactions, and continuous effects of sire FEC EBV. The FEC and PCV of offspring was positively ($P < 0.001$) and negatively ($P < 0.001$), respectively, related to the sire WFEC and PFEC. A second objective was to examine effects on sale prices of breeding-quality ram lambs from four farms, including ARS, of lamb EBV for WFEC and a ewe productivity trait (**EPT**) designed to identify ewes with superior maternal ability. Sale price effects were dominated by sale type with a premium of $1086/head relative to direct sales from the farm for animals in NSIP or Katahdin Hair Sheep International Expo sales. Producers likewise assigned a premium of $107/head to animals retained for use in their own breeding herds. The next most impactful variable was the EPT EBV. A 1-SD increase of 2.3 units in EPT yielded an extra $39/head whereas a similar 1-SD decrease in EPT resulted in a $32/head discount. Lambs born in fall were discounted by $6/head relative to those born in winter. Lambs that were not dewormed received a $29/head premium over lambs that were dewormed and was presumably taken as a phenotypic signal that the lamb was resistant. A ± 1-SD change in WFEC had no effect on sale value, which changed by less than $0.01/head. This result may have been confounded with whether or not the lamb had been dewormed. Thus, while more parasite-resistant sires produced offspring with lower FEC, the sale value of these ram lambs appeared to have been more strongly associated with other EBV such as EPT or with a desire to obtain ram lambs with balanced EBV rather than elite EBV for parasite resistance.

1. Introduction

Infection with gastrointestinal nematodes (**GIN**) threatens economic viability of small ruminant production in warm, humid climates and is a major health concern due to widespread anthelmintic resistance (Howell et al., 2008; Kaplan and Vidyashankar, 2012). Gastrointestinal nematode infection can cause reduced weight gains, anemia, and death. Interventions such as the use of copper oxide wire particles, improved forage programs, optimal nutrition, and, perhaps most notably, genetic selection for parasite resistance in the animal are important alternatives

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to anthelmintic treatment (Woolaston and Baker, 1996; Terrill et al., 2012; Burke and Miller, 2020).

The National Sheep Improvement Program (**NSIP**) provides genetic evaluation information to the American sheep industry by converting performance records into relevant decision-making tools (www.nsip.org). Estimated breeding values (**EBV**) are calculated for each individual enrolled in NSIP and provide science-based, industry-tested predictions of animal genetic merit.

Significant progress has been made in identifying sheep that are superior for parasite resistance in the last few years. This innovation was based primarily on fecal egg count (**FEC**) EBV (Notter, 1998) and facilitates sustainable pasture-based and organic sheep production by reducing GIN infection and need for deworming. Coupling genetic resistance with other important growth, reproductive, and maternal traits, permits development of economically productive, parasite-resistant flocks (Ngere et al., 2018; Notter et al., 2018).

The Katahdin hair sheep breed is a composite developed in the 1950 s, now used as a dual purpose breed (maternal, meat). It became popular in the U.S. because of its reputation for a high degree of parasite resilience and/or resistance (Ngere et al., 2018; Notter et al., 2018), high fertility, high fecundity, strong maternal traits, and the ability to shed its hair coat. It ranks among the top six breeds for numbers of sheep registered in the U.S. from 2002 to 2020 (Katahdin Hair Sheep International, 2020) and has the most FEC data included in NSIP compared with other U.S. breeds.

Assessment of livestock value is difficult because of the number and complexity of factors that influence value (Buccola, 1980). Hedonic modeling, however, provides a straightforward means of quantifying the impact of specific traits on prices of both market animals and breeding stock. Hedonic analysis was initially used to study relationships between feeder cattle auction prices and observable physical characteristics of the cattle such as weight, breed type, and sex (e.g., Faminow and Gum, 1986; Schroeder et al., 1988; Turner et al., 1991). The methodology was also relatively quickly adapted to assess the value of credence attributes such as source verification or vaccination status (Coatney et al., 1996; Lawrence and Yeboah, 2002; Williams et al., 2012; Zimmerman et al., 2012). In a recent investigation of feeder cattle prices in Tennessee, Martinez et al. (2021) employed a hedonic pricing model to value a health-related attribute of feeder cattle (tested for persistent infections with bovine viral diarrhea) and found a positive and significant premium associated with this information.

Hedonic pricing models have also been used to evaluate factors influencing prices of breeding stock. Most of these studies focused on beef cattle (Parcell et al., 1995, 2006; Dhuyvetter et al., 1996; Mitchell et al., 2018; Boyer, et al., 2019). However, similar models have been used to assess value in dairy bulls (Schroeder et al., 1992; Richards and Jeffrey, 1996), brood mares (Neibergs, 2001) and breeding boars (Walburger and Foster, 1994).

Few studies in the literature have applied hedonic pricing models to small ruminants. Small ruminant markets received some attention in developing countries, but primarily for market animals rather than breeding stock (e.g., Jabbar, 1998; Ahmad et al., 2018). Virtually all of the literature on hedonic pricing has focused on either observable traits (e.g, weight, color, sex), credence attributes (vaccination status, origin), or, for breeding stock, EBV for key production traits such as average daily gain or milk production. Apart from Martinez et al. (2021), evaluation of traits related directly to health and mortality are almost absent in the literature.

The objective of this study was to determine the value of selection for parasite resistance. Specific goals were to quantify the impact of the sire's FEC EBV on GIN infection markers (FEC, PCV, incidence of deworming, and body weight) of offspring, and estimate impact of parasite resistance on prices of breeding-quality ram lambs. Ram sales were analyzed using a hedonic pricing model to estimate the impact of FEC EBV and of the Katahdin ewe productivity index (Vanimisetti et al., 2007) on ram prices. The model also considered effects on price of fall vs. winter lambing, whether or not a lamb was dewormed prior to sale, and whether the animal was retained to join the breeding herd, sold in various premium sale events, or sold as a market animal.

2. Materials and methods

2.1. Experimental animals

All experimental procedures were reviewed and accepted by the Agricultural Research Service Animal Care and Use Committee in accordance with the *Guide for the Care and Use of Agricultural Animals in Research and Teaching* (ADSA-ASAS-PSA, 2020). Pain and stress to animals were minimized throughout the experimental period.

Katahdin sheep have been maintained at USDA, Agricultural Research Service, Dale Bumpers Small Farms Research Center in Booneville, AR (**ARS**; located at 35.1 N, −93.9 W) since 1999. The flock was enrolled in the NSIP in 2009 with historical data entered since 2001. Breeding rams were generated from within the ARS flock or obtained from other flocks enrolled in the NSIP and selected for parasite resistance using FEC EBV with balanced EBV for reproduction and growth traits identified using the NSIP Katahdin percentile report (www.nsip.org). In October 2021, the NSIP offered genomic-enhanced EBV (**GEBV**) derived from a Katahdin reference population (McMillan et al., 2022) to increase accuracies of prediction of EBV (Rupp et al., 2016; Van der Werf et al., 2017). Concomitantly, parameter values in calculating EBV also changed leading to lower accuracies which the genomic data buffered (Table 1). Weaning (**WFEC**) and post-weaning (**PFEC**) FEC EBV determined in September 2021 [using performance and pedigree (**P**) without genomic (**G**) information; **$WFEC_P$**, **$PFEC_P$**, respectively] and October (**$WFEC_G$** and **$PFEC_G$**, respectively) were included as estimates of GIN resistance (Table 1). Published FEC EBV were obtained by cube-root transformation of individual FEC and their inclusion in a multi-trait genetic analysis with other NSIP production traits (Brown et al., 2007). Resulting FEC EBV on the cube-root scale were then converted to a percentage of the mean FEC for reporting (Notter, 2013). The FEC EBV of the sires represented in this study (Table 1) ranged from − 27 to − 101% for WFEC and from − 53 to − 101% for PFEC. The theoretical minimum for FEC EBV was − 100% but accumulated rounding events produced a minimum FEC EBV of − 101%. The FEC EBV were similar for performance-based and genome-enhanced EBV. Based on the July 2022 Katahdin FEC EBV percentile report, these EBV corresponded to animals in approximately the 40th to 99th percentiles for WFEC and the 60th to 99th percentiles for PFEC.

Ewes were bred to lamb in winter (early January to mid-February) of 2018, 2019, 2020, and 2021, or fall (early October to mid-November) of 2018, 2019, and 2020 with a 31–46 day lambing period. Sire of lamb was identified or confirmed by genotyping using a Sheep Parentage 160 K or GeneSeek® Genomic Profiler™ Ovine 50 K (Neogen Corp., Lincoln, NE) array. Only sires with offspring that survived to at least 60 days of age and had $\geq$ 9 lambs were used. Offspring from one sire were removed because his WFEC and PFEC EBVs were more than 2 SD larger than those of the other sires, thus creating an outlier. The remaining 23 sires were used among all years, with 9–97 offspring per sire (Table 1). In winter lambing of 2018, 2019, 2020, and 2021 (**W18**, **W19**, **W20**, **W21**), there were a maximum of 138, 90, 65, and 85 offspring, respectively, at each time point (60, 90, 120, 150 days of age); in fall lambing of 2018, 2019, and 2020 (**F18**, **F19**, **F20**), there were 124, 155, and 180 offspring, respectively.

Lambs were vaccinated against *Clostridium* spp. (5 ml Covexin® 8, Intervet, Inc., Omaha, NE) and caseous lymphadenitis (2 ml Case-Bac, Colorado Serum Co., Denver, CO) at approximately 60 days of age and received 2 ml boosters 6–8 weeks later.

Lambs grazed mixed grass pastures (predominantly bermudagrass in late spring and summer and tall fescue in cooler months) and were naturally infected with GIN. Depending on forage quality and availability, lambs were supplemented with 250 (first 30 days after weaning)

Table 1
Number of offspring per sire, estimated breeding value (EBV), and accuracies (expected correlations between actual and estimated breeding values x 102) for fecal egg count (FEC) weaning (WFEC) and post-weaning (PFEC) EBV calculated in September 2021 for performance-based EBV (WFECP and PFECP) and October 2021 for genome-enhanced EBV (WFECG and PFECG).

Sire	n	$WFEC_P$	Accuracy	$PFEC_P$	Accuracy	$WFEC_G$	Accuracy	$PFEC_G$	Accuracy
14155	22	-94	93	-96	95	-90	92	-98	92
16080	68	-96	93	-100	96	-96	90	-100	94
16162	13	-36	84	-73	89	-50	80	-80	83
16604	21	-101	94	-101	95	-100	92	-100	92
16836	97	-52	93	-76	96	-37	92	-27	93
17012	84	-27	90	-53	94	-43	86	-55	90
17036	33	-82	87	-96	90	-76	83	-92	84
17080	31	-64	91	-73	92	-66	88	-71	80
17083	24	-67	83	-71	89	-69	77	-72	71
17170	19	-33	85	-69	88	-29	80	-70	82
18015	47	-88	90	-98	93	-76	87	-77	88
18036	83	-36	94	-88	95	-13	92	-47	91
18053	9	-77	81	-85	85	-60	75	-68	77
18084	18	-88	84	-99	89	-60	78	-72	81
18309	38	-37	85	-66	89	-44	82	-19	82
19029	41	-83	88	-88	92	-72	84	-60	86
19063	29	-74	86	-97	90	-74	81	-85	84
19070	31	-50	88	-88	91	-50	84	-69	85
19071	55	-93	90	-98	93	-92	88	-91	89
19108	20	-95	83	-99	86	-93	81	-93	82
19131	10	-91	83	-99	86	-80	77	-83	78
19184	15	-81	85	-99	88	-75	80	-92	81
20031	29	-51	86	-83	89	-26	80	-56	82

to 500 g/head daily a mixture of peas, alfalfa pellets, soyhulls and free choice trace mineral (Redmond Minerals with Selenium-90, Inc., Redmond, UT; 2018) or with a corn, soybean meal or a corn, oats, soybean mixture that included trace minerals (2019, 2020, 2021) starting at approximately 60–150 days of age with the objective of maintaining body condition score at 3.5 (1 = thin; 5 = fat). Lambs always had access to water. Lambs were weaned at 65 (W20, W21) or 95 days of age (W18, F18, W19, F19, F20) by fence line contact with dams.

2.2. Data collection for GIN and body weight measures

Feces were collected directly from the rectum to determine FEC using a modified McMaster technique with a sensitivity of 50 eggs/g (Whitlock, 1948), and blood from the jugular vein was used to determine blood packed cell volume (**PCV**). Feces and blood were collected and body weight and FAMACHA scores (Kaplan et al., 2004) determined at approximately 60, 90, 105, 120, 135, and 150 days of age, but not all lamb groups were sampled at every measurement time in all years. Genera of GIN from pooled samples were determined by coproculture (Peña et al., 2002). Weaning data are entered into NSIP between 42 and 90 days of age when mean FEC of lambs within a season are above 500 eggs/g ideally. Post-weaning data are generally submitted after 151 days of age (nsip.org).

Lambs were dewormed if anemic (PCV $<$ 19% or FAMACHA score $>$ 3) or the body condition score was $<$ 2.5, and data were excluded for 30 days after deworming. Lambs were dewormed with 1 g copper oxide wire particles (COWP; Copasure; Animax Veterinary Technology, UK) in a gelatin capsule (Burke and Miller, 2006) in combination with albendazole (15 mg/kg BW; Valbazen®, Zoetis Animal Health, Kalamazoo, MI; Burke et al., 2016) and levamisole (Prohibit®, 8.0 mg/kg; Huvepharma, Inc., St. Joseph, MO). If diarrhea was observed, sulfadimethoxine (0.77 g/kg body weight for 3 days; 12.5% Di-Methox, AgriLabs, St. Joseph, MO) and electrolytes (0.66 ml/kg Nutri-Drench®, Bovidr Laboratories, Inc., Scottsbluff, NE) were administered. If diarrhea did not improve within 3 days, lambs were dewormed as described above. Deworming treatment associated with diarrhea occurred in one W18, 14 F18, 8 W19, four F19, and one W20 lamb. Only one lamb was dewormed before 90 days of age. Estimated efficacy against *H. contortus* was 0% for benzimadazoles, between 65% and 85% for levamisole, and more than 95% for moxidectin in 2019 (Drenchrite performed by R. Kaplan, University of Georgia). Anthelmintic resistance of *Trichostrongylus* spp. was detected for benzimadazoles and levamisole.

2.3. Statistical analyses of measures of GIN resistance and body weight

Data were analyzed using the mixed model procedure of SAS 9.4 (SAS Institute, Cary, NC) with repeated measures and an autoregressive covariance structure. The mathematical model for PCV, FEC, FAMACHA scores, and body weight included fixed effects of season, year, sex, birth type (single or multiple born), age of dam (1, 2, 3, or $\geq$ 4 years of age), day as a repeated measure, and their significant ($P < 0.05$) interactions. Correction for age of lamb was achieved by fitting birth date within each season as a covariate, and models were run with and without the sire FEC EBV as a covariate. FEC data were transformed as ln(FEC + 25) for analysis, but means were back-transformed for presentation. General linear models in SAS were used to test differences in average daily gain (**ADG**) from birth to 60 days of age (**ADG_1**) and 60–150 days of age (**ADG_2**), and the proportion of lambs that required deworming, including season, year, sex, birth type, age of dam, and interactions in the model. Means were separated using the PDIFF option with $P < 0.05$.

2.4. Estimate of value of lamb EBV

In a separate study, sale data on rams was collected from the ARS flock (37 lambs born in fall and 49 in winter; described above) and 3 private flocks (lambs born January to March) enrolled in NSIP between 2018 and 2020 (Table 2). The sales data from the four flocks contained 194 observations for lambs born from 2018 to 2020. Data included birth date, weaning and post-weaning body weights and dates, whether the ram lamb had been dewormed, registration status (fully registered within the breed registry or not), whether animal was sold or retained by the farm for breeding, date of sale, and price obtained. A NSIP EBV report within 90 days of the sale was used for values of WFEC (FEC collected between 42 and 90 days of age) and Ewe Productivity Trait (**EPT**), a prediction of genetic merit for total weight of lambs weaned per ewe lambing. Animals sold at local auctions were not considered. Removal of lambs with missing or extreme data left a final data set of 175 ram lambs.

Using generalized regression neural networks (**GRNN**) as an Add-in to Excel (Neural Tools® v7.5; Palisade, 2018), sale price of sheep was

Table 2
Number of rams sold for breeding between 2018 and 2020 from the USDA Agricultural Research Service (ARS) flock and three private farms (A, B, C).

						Dewormed	
Flock	n	Retain	Farm	NSIP	KHSI	No	Yes
ARS	86	17	60	2	7	22	64
A	17	1	10	0	6	5	4
B	32	0	32	0	1	6	23
C	59	9	43	0	7	58	1

Animals were retained on farm, sold by private treaty from the farm (ARS sold rams by competitive bidding from farm using an online auction service), sold in a premium National Sheep Improvement Program (NSIP) sale or a Katahdin Hair Sheep International (KHSI) Expo sale (based on competitive bidding), all based on NSIP estimated breeding values and acceptable phenotypic traits. Deworming occurred in some animals prior to sale (not indicated in some animals in Flocks A and B).

estimated to be a function of.

$$P = f(ST, WORM, SEASON, WFEC, EPT), \quad (1)$$

where, sale type (**ST**) was a categorical variable that could vary from i) 'None' in case of retention; ii) 'Farm' when buyers purchased on farm; or iii) 'NSIP' involving NSIP in the sale including 'KHSI (Katahdin Hair Sheep International Expo sale)/Premium sale' for a special sale designation, WORM was a binary 0/1 variable about whether the animal was dewormed (1) or not (0), SEASON was a binary 0/1 variable capturing time of birth in the fall (0 = Sep. – Dec.) or winter (1 = Jan. – Mar.), WFEC and EPT were EBV values for WFEC and the EPT, respectively. The EPT equation is [100 + (0.246 × WWT) + (2.226 × MWWT) + (−3.5 × NLB) + (40.6 × NLW)], where NLB is number of lambs born, NLW is the number of lambs weaned, WWT is the weaning weight, and MWWT is the maternal weaning weight. Sale price of retained ram lambs was determined by the farmer if they were to have sold the ram to another farmer.

Neural network analysis or genetic algorithms employing GRNN avoided having to impose a functional form on the regression analysis. Enabling live predictions® in the tool allowed estimation of sale premia as a function of modifying a particular variable holding all other variables at their mean value or at the modal observation for categorical data (e.g. ST, WORM and SEASON).

Further, GRNN calculates the relative impact (**RI**) of individual explanatory variables as follows:

$$RI_i = \Delta_i \Big/ \sum_{i=1}^{n} \Delta_i \quad (2)$$

where Δ_i is the range of estimated sale price outcomes that occurs when altering the explanatory variable *i* from their minimum to their maximum value holding all other explanatory variables constant and n is the number of explanatory variables. The i^{th} impact on sale price relative to the sum of all explanatory variable impacts becomes the relative impact RI_i. Relative impacts sum to 100% across all explanatory variables.

3. Results

3.1. Trends in GIN measures and growth among seasons and years

Mixed genera of GIN were present within and among coprocultures. Larval cultures derived from lambs sampled between December and June were 3–97% *H. contortus*, 2–97% *Trichostrongylus* spp., 0 (none observed) to 59% *Cooperia* spp., and 0–22% *Oesophagostomum* spp. Proportions of each genera present were not clearly dependent on the month or season of sampling (data not shown).

The FEC were influenced by season × year × day of age interaction

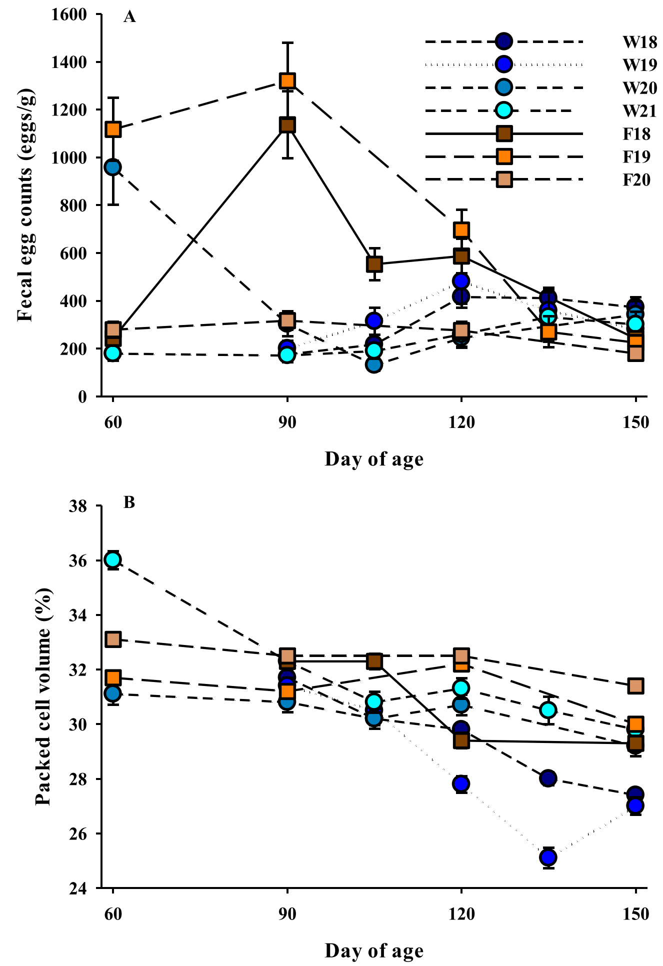

Fig. 1. Least squares means and standard errors of back-transformed fecal egg counts (Panel A) and packed cell volume (Panel B) of lambs born in winter (January – February; open circles) of 2018 (W18), 2019 (W19), 2020 (W20), and 2021 (W21), and fall (October – November; closed squares) of 2018 (F18), 2019 (F19), and 2020 (F20) and sampled at approximately 60, 90, 105, 120, 135, and 150 days of age.

($P < 0.001$; Fig. 1A) with markedly higher values at 60 days of age in F19 and W20, and at 90 days of age in F18 and F19 compared with other season-year-day of age groups. Differences in FEC among seasons and years after 120 days of age were still different between F18 and W18, W19, and W21, between F19 and winter in all years, and between F20 and winter in all years (PDIFF, 150 days of age, $P < 0.01$) with fall FEC being less than winter FEC at that time (Fig. 1A).

Higher mean FEC were not associated with mean PCV values that indicated problems with anemia at 60 or 90 days of age, but W18 and W19 lambs had lower PCV at 120, 135 and 150 days of age (season × year × day of age, $P < 0.001$; Fig. 1B). Based on PCV values of 19% or less, which was a criterion used to indicate need for deworming (Kaplan et al., 2004), only one lamb within each season (F18 at 120 days of age, F20 at 150 days of age, W19 at 135 days of age, W18 at 150 days of age), or two in F19 (one at 60 days and one at 150 days of age) required deworming associated with anemia. FAMACHA scores were influenced by a season × year × day of age interaction with peak values (indicating greater incidence of anemia) in W20 and W21 at 90 days of age and in W18 at 120 and 135 days of age ($P < 0.001$; Fig. 2). FAMACHA scores of winter lambs generally increased over time between 60 and 150 days of age and were higher than those of fall lambs.

Overall, only 4.2% of lambs required deworming based on our selective criteria. There was a season × year effect ($P < 0.001$) and age of dam effect ($P < 0.05$) on incidence of deworming, but none of the other

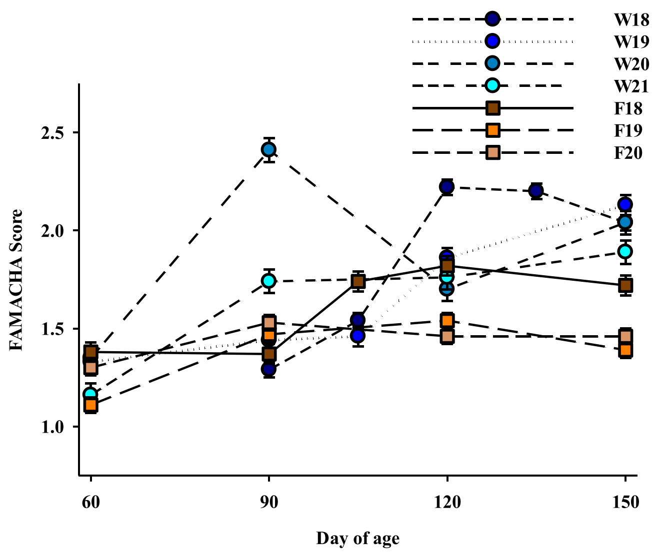

Fig. 2. Least squares means and standard errors of FAMACHA scores of lambs born in winter (January – February; open circles) of 2018 (W18), 2019 (W19), 2020 (W20), and 2021 (W21) or fall (October – November; closed squares) of 2018 (F18), 2019 (F19), and 2020 (F20). Scores were determined at approximately 60, 90, 105, 120, 135, and 150 days of age.

variables influenced this measure. More lambs required deworming in F18 (13.6 ± 2.1%) and W19 (11.8 ± 2.1%) than any of the other seasons. Least squares means for remaining year-season groups ranged from 0.1% to 5.2% and did not differ. Lambs from older ewes (more than 3 years of age) required no deworming, while offspring from yearling, 2 and 3-years of age required 7.2 ± 2.2%, 4.8 ± 1.2%, and 4.3 ± 2.0%, respectively.

Body weights of lambs were influenced by season × year × day of age interaction ($P < 0.001$; Fig. 3) and by all other variables (sex, birth type, age of dam) in the model ($P < 0.001$). Season × year interaction ($P < 0.001$) influenced ADG_1 mostly because of lower ADG in F19 and higher ADG in F20 and W21 (Table 3), and all other variables in the model were significant ($P < 0.001$). The ADG_1 was lower in twin than single born and reared lambs (data not shown), and in offspring from yearling ewes (232.2 ± 4.6 g/day), and higher in offspring from ewes older than 3 years of age (273.4 ± 3.2 g/day; 2-year old, 252.2 ± 2.6 g/day; 3-year old, 255.0 ± 4.1 g/day). Season × year interaction ($P < 0.001$) was also present for ADG_2, with highest gains in F19 and lowest gains in F18 (Table 3). Birth type and age of dam did not influence ADG_2, but males grew faster than females (data not shown).

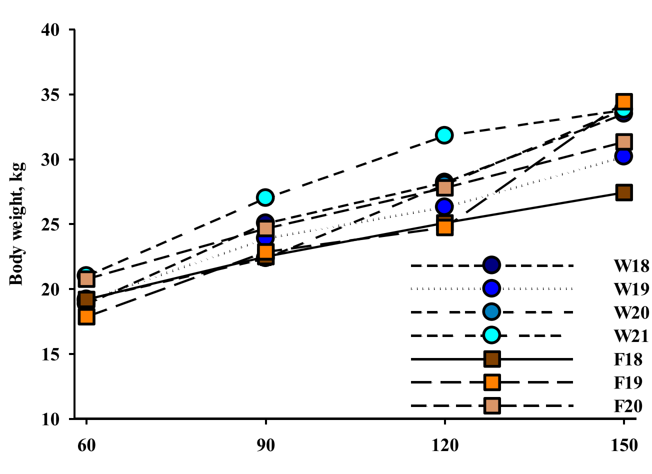

Fig. 3. Least squares means and standard errors of body weight of lambs born in winter (January – February; open circles) of 2018 (W18), 2019 (W19), 2020 (W20), and 2021 (W21) or fall (October – November; closed squares) of 2018 (F18), 2019 (F19), and 2020 (F20) and weighed at approximately 60, 90, 120, and 150 days of age.

Table 3
Least squares means and standard errors of average daily gain (ADG) of lambs born in winter (January – February; W) of 2018, 2019, 2020, and 2021, and fall (October – November; F) of 2018, 2019, and 2020 estimated from body weight determined at birth to ~60 days of age (ADG_1) and from and ~60–150 days of age (ADG_2). Means with different letters within age groups differ ($P < 0.01$).

	ADG_1 Season		ADG_2 Season	
Year	F	W	F	W
2018	255.5 ± 4.5^{bc}	249.1 ± 4.0^{b}	95.7 ± 3.7^{a}	168.7 ± 3.2^{d}
2019	225.5 ± 3.6^{a}	243.8 ± 4.6^{b}	195.8 ± 2.9^{e}	132.6 ± 3.9^{b}
2020	265.4 ± 3.7 ^{cd}	245.1 ± 5.7^{b}	124.0 ± 3.0^{b}	173.4 ± 4.6^{d}
2021	–	269.8 ± 5.1^{d}	–	149.4 ± 4.1^{c}

Need for deworming was negatively correlated with ADG_1 ($r = -0.11$, $P = 0.001$) and ADG_2 ($r = -0.16$, $P < 0.001$) but not correlated with sire FEC EBV.

3.2. Influence of sire FEC EBV on GIN measures and growth

Continuous effects of sire $WFEC_P$, $PFEC_P$, $WFEC_G$ and $PFEC_G$ significantly influenced lamb FEC (all $P < 0.001$). Regression equations for each season of birth were generated to understand how the performance or genomic-enhanced WFEC or PFEC of the sire influenced the offspring FEC (Table 4). The FEC of offspring was positively related to their sire $WFEC_P$ or $WFEC_G$ and $PFEC_P$ or $PFEC_G$; there was a decrease in offspring FEC as sire WFEC and PFEC decreased or became more negative (favorable), whereas − 100 is considered to be the highest GIN resistance (Table 4). Using back-transformed FEC (which yields lower values than raw data), the reduction in FEC of offspring born in fall or winter (season, $P < 0.001$) in response to sire FEC EBV between − 100 and − 30 can be shown in Fig. 4. The FEC were greater in winter lambs with predicted values of 281 and 185 eggs/g more in $WFEC_P$ and $WFEC_G$, respectively, and 557 and 205 eggs/g more in $PFEC_P$ and $PFEC_G$, respectively, between the − 100 and − 30 sire EBV.

Similar to FEC, continuous effects of sire $WFEC_P$, $PFEC_P$, $WFEC_G$ and $PFEC_G$ influenced lamb PCV (all $P < 0.001$). The predicted relationships between lamb PCV and sire EBV were linear (Table 4). There was an inverse relationship between PCV and sire FEC EBV in that there was a reduction in offspring PCV of 1% or 0.7% between the − 100 and − 30 $WFEC_P$ and $WFEC_G$, respectively, and 2.6% and 0.9% in $PFEC_P$ and $PFEC_G$ indicating that lambs with lower sire FEC EBV were less anemic and therefore more resilient to GIN. FAMACHA is a less sensitive, or a subjective measure of anemia compared with PCV with most scores falling between 1 and 3. In that model, the $PFEC_P$ ($P = 0.03$; fall R^2, 0.07; winter R^2, 0.17), but not the $WFEC_P$ ($P = 0.22$) covariate was significant. When $PFEC_P$ was included in the model, there was a 0.12 unit increase as sire became less resistant. Including $WFEC_G$ ($P = 0.02$; fall R^2, 0.08; winter R^2, 0.16), but not $PFEC_G$ ($P = 0.72$) showed that the correlation was positive, in contrast to the PCV analysis.

Offspring body weights recorded between 60 and 150 days of age were significantly or tended to be associated with sire $WFEC_P$ ($P = 0.08$), $WFEC_G$ ($P = 0.03$), or $PFEC_G$ ($P = 0.04$; Table 4) but not $PFEC_P$ ($P = 0.89$). There was a nominal increase in lamb weights between sires $WFEC_G$ between − 100 and − 30 of 0.75 kg and sire $PFEC_G$ of 0.79 kg. The ADG_1 was not influenced by sire FEC EBV, but ADG_2 was positively correlated with sire $WFEC_G$ ($P < 0.004$; fall R^2, 0.11; winter R^2, 0.02), and sire $PFEC_G$ ($P < 0.007$; fall R^2, 0.13; winter R^2, 0.02; Table 4), but not $WFEC_P$ or $PFEC_P$. However, because the sire EBV

Table 4
Regression equations to predict offspring fecal egg count (FEC; log transformed), blood packed cell volume (PCV), body weight between 60 and 150 days, and post-weaning average daily gain (ADG2) from performance-based or genome-enhanced sire FEC estimated breeding value (EBV).

Sire EBV	Equatione	R^2	*P*<
FEC (y)			
Fall born			
$WFEC_P$	$y = 5.58 + 0.0095x$	0.095	0.001
$PFEC_P$	$y = 6.44 + 0.016x$	0.089	0.001
$WFEC_G$	$y = 5.37 + 0.0086x$	0.107	0.001
$PFEC_G$	$y = 5.65 + 0.086x$	0.112	0.001
Winter born			
$WFEC_P$	$y = 6.64 + 0.0095x$	0.081	0.001
$PFEC_P$	$y = 7.20 + 0.016x$	0.071	0.001
$WFEC_G$	$y = 6.27 + 0.0086x$	0.086	0.001
$PFEC_G$	$y = 6.37 + 0.086x$	0.070	0.001
PCV (y)			
Fall born			
$WFEC_P$	$y = 30.3–0.015x$	0.066	0.001
$PFEC_P$	$y = 27.6–0.037x$	0.074	0.001
$WFEC_G$	$y = 30.8–0.0105x$	0.064	0.001
$PFEC_G$	$y = 30.2–0.013x$	0.066	0.001
Winter born			
$WFEC_P$	$y = 28.2–0.015x$	0.302	0.001
$PFEC_P$	$y = 25.8–0.037x$	0.301	0.001
$WFEC_G$	$y = 28.6–0.0105x$	0.309	0.001
$PFEC_G$	$y = 28.3–0.013x$	0.307	0.001
BW (y)			
Fall born			
$WFEC_G$	$y = 21.7 + 0.011x$	0.50	0.001
$PFEC_G$	$y = 22.0–0.011x$	0.50	0.001
Winter born			
$WFEC_G$	$y = 24.3–0.011x$	0.50	0.001
$PFEC_G$	$y = 24.4–0.011x$	0.50	0.001
ADG_2 (y)			
Fall born			
$WFEC_G$	$y = 185.3 + 0.183x$	0.11	0.004
$PFEC_G$	$y = 187.0 + 0.179x$	0.13	0.007
Winter born			
$WFEC_G$	$y = 210.8 + 0.183x$	0.02	0.004
$PFEC_G$	$y = 210.5 + 0.179x$	0.02	0.007

Dependent variables and FEC EBV are designated as y and x, respectively. Sire FEC EBV include weaning (WFEC) and post-weaning (PFEC) FEC EBV based on only phenotypic measurements (P) and calculated in September 2021 or genome-enhanced (G) in October 2021.

estimate was so low, there was little actual impact on changes in ADG_2 between resistant and more susceptible sires.

3.3. Influence of lamb EBV on value of the lamb

Summary statistics (Table 5) indicated that sales transactions were dominated by on-farm sales of NSIP-enrolled animals that were predominantly resistant to GIN but with approximately half of the animals dewormed prior to sale (animals were not necessarily dewormed based on selective criteria described previously). Average and SD of lamb EBV were used to estimate premia and discounts when animals deviated from the average EBV. For other attributes, such as sale type, birth season, and whether lambs were dewormed prior to sale, a premium or discount was established relative to the most frequent attribute.

Neural networks are trained using a randomly selected subset of the records to develop the necessary prediction equation, and the remainder of the observations are used to test the predictive accuracy of these equations. Alternative sampling schemes were therefore compared to estimate the effect of the percentage of observations for training. Sensitivity analysis indicated that the prediction errors, measured by R^2, were least when 80% of observations were used for training and 20% of observations were used to test the trained network. Since observations used for training are drawn randomly from the available data, model outcomes from 10 trained networks were used to predict premia and

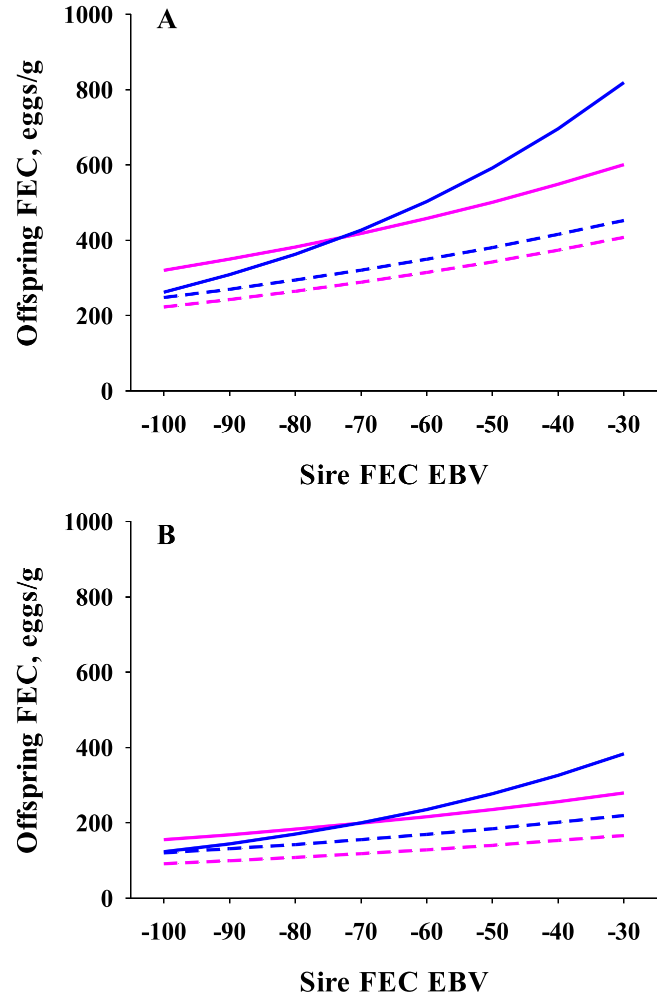

Fig. 4. Regression curves describing the observed linear relationship ($P < 0.001$) between fecal egg counts (FEC) of offspring born in winter (Panel A) or fall (Panel B) and sire weaning FEC estimated breeding value (EBV) derived from performance-based ($WFEC_P$; pink line) and genome-enhanced ($WFEC_G$; blue line) EBV.

discounts for attributes of these ram lambs (Table 6). The relative impact of each of the explanatory variables is depicted in Fig. 5. Sale type had the largest influence on sale price. Premiums for NSIP and or KHSI sales ($1086/head) were larger than those associated with farm sales. Animals retained for breeding on the farm were also valued more highly ($107/head) than those sold on the farm. Second in relative impact was the EPT EBV (Fig. 5). Premia and discounts for ± 1 SD changes in EPT EBV were $39/head and -$32/head, respectively (Table 6). The WFEC had little sale impact in sale price projections that differed by < $0.01/head and favored lambs with higher (i.e., less desirable) WFEC. Whether the animal was dewormed was tertiary in relative impact and resulted in an average $29/head premium for animals that were not dewormed. Fall-born lambs had a lower value than winter-born lambs, discounted by an average of $46/head.

4. Discussion

Given the high prevalence of anthelmintic resistance in the ARS flock and across the U.S. (Howell et al., 2008; Kaplan and Vidyashankar, 2012), the importance of genetic resistance to GIN is clear. The concept is not new, and selection for GIN resistance has been shown to be effective in wool sheep (Woolaston et al., 1990; Woolaston and Baker, 1996; Zvinorova et al., 2016). No similar study has been conducted to examine the impact of parasite resistance EBV and their influence on the

Table 5
Summary statistics and sale price predictions using categorical and cardinal observations related to lamb characteristics for 175 ram lambs born between 2018 and 2020.

Description	Average	SD	n
Sale Price (*P*) ($/head)	713.03	707.80	175
Sale Type (*ST*)			
Farm	na	na	129
KHSI/Premium	na	na	20
None (Retained)	na	na	26
Birth Season (*SEASON*)			
Oct – Nov (Fall)	na	na	37
Jan – Mar (Winter)	na	na	138
Dewormed (*WORM*)			
Yes	na	na	93
No	na	na	82
EBV Values			
WFEC	-74.33	26.06	175
EPT	106.96	2.31	175
WWT	1.83	0.80	175
PWWT	3.28	1.62	175
MWWT	0.77	0.43	175
NLW	13.20	7.38	175

The rams were derived from editing an original data set of 194 sale transactions from four Katahdin flocks. ST was a categorical variable that took values of i) 'None' for lambs that were retained for breeding; ii) 'Farm' when buyers purchased the ram on the farm; iii) 'NSIP' for rams sold in an National Sheep Improvement Program (NSIP) sale; or iv) 'KHSI Premium sale' for rams sold in a Katahdin Hair Sheep International (KHSI) Premium sale, SEASON was a binary 0/1 variable indicating whether the animal was born in winter (1) or fall (0), WORM was a binary 0/1 variable indicating whether the animal was wormed prior to sale (1) or not (0), WFEC,EPT, WWT, PWWT, MWWT, and NLW were EBV values for weaning fecal egg count, ewe productivity trait, weaning weight, post-weaning weight, maternal weaning weight, and number of lambs weaned, respectively. Because the EPT EBV is a function of EBV for weaning weight, number of lambs weaned and maternal traits [EPT = 100 + (0.246 × WWT) + (2.226 × MWWT) + (−3.5 × NLB) + (40.6 × NLW)], statistics describing the latter four EBV are presented for information only but were not used to predict sale prices.

sale value of breeding stock. Most of the data for derivation of parasite resistance EBV in the U.S. were from Katahdin sheep (Notter, 2011; Ngere et al., 2018; Notter et al., 2018), although any breed of sheep or goats can submit FEC data to NSIP. Under natural GIN exposure, the heritability of FEC is moderate (Ngere et al., 2018), in association with the large variability in FEC commonly observed within a contemporary group, but genetic improvement in parasite resistance can be achieved by retention of superior animals or purchase of resistant stock.

The GIN infection in the ARS lambs was initially more intense (i.e., FEC were higher) in fall-born lambs than in winter-born lambs, though these higher FEC were not accompanied by elevated incidence of anemia. In this environment, fall-lambing ewes had greater GIN exposure in warm late summer and early fall months and grazed poorer quality forages (i.e., dormant or late season bermudagrass, which has low protein content). However, fall-born lambs typically had access to higher-quality cool-season forage by 60–90 days of age which potentially

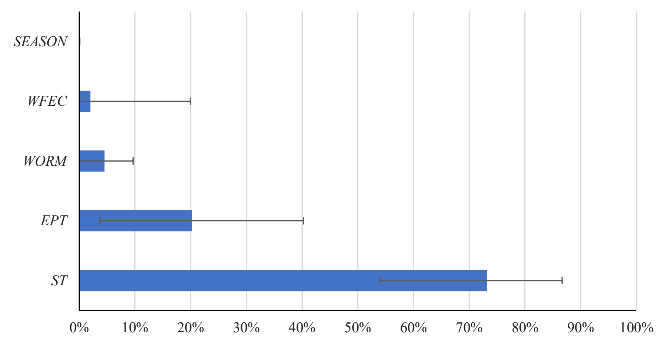

Fig. 5. Relative impact of explanatory variables used to predict sale prices of lambs. Error bars depict minimum and maximum relative impact across ten model runs [Eq. (2)]. Sale type (ST) was a categorical variable that could vary from i) 'None' in case of retention; ii) 'Farm' when buyers purchased on farm; 'NSIP' involving NSIP in the sale; or iv) 'KHSI/Premium sale' for a special sale designation. Since so few NSIP sale type data points were available, both NSIP and KHSI/Premium sales were lumped into a 'Premium' category. SEASON was a binary 0/1 variable indicating whether the animal was born in winter (1) or not (0). WORM was a binary 0/1 variable about whether the animal was wormed prior to sale (1) or not (0). WFEC and Ewe Productivity Index (EPT) were estimated breeding values (EBV) for weaning fecal egg count and ewe productivity trait. The KI EBV value captures weaning weight, number of lambs weaned and maternal traits.

Table 6
Summary of estimated premia and discounts for lamb attributes holding all other attributes at their average or modal value for lambs born from four farms between 2018 and 2020 across 10 model runs using generalized regression neural networks.

Model Run	1	2	3	4	5	6	7	8	9	10	Avg.
Explanatory Variables	Premium/ (Discount) in $/head relative to selling a dewormed lamb on the farm that was born in winter with average EPT and WFEC EBV values										
SEASON	($0.41)	($53.19)	($0.07)	($0.09)	($0.23)	($0.23)	($0.77)	($0.10)	($0.38)	($0.02)	($5.55)
WORM	$23.60	$0.67	$37.84	$28.62	$41.62	$14.23	$45.06	$40.77	$21.55	$40.61	$29.46
EPT+	$33.39	$27.83	$44.63	$16.17	$9.11	$34.68	$43.89	$114.95	$27.93	$36.58	$38.92
EPT-	($29.29)	($31.79)	($31.61)	($14.51)	($8.20)	($32.10)	($26.94)	($94.95)	($25.21)	($28.19)	($32.28)
WFEC+	$0.00	$0.01	$0.02	$0.00	$0.00	($0.00)	$0.01	($0.00)	$0.01	$0.00	$0.00
WFEC-	($0.00)	($0.01)	($0.02)	($0.00)	($0.00)	$0.00	($0.01)	$0.00	($0.01)	($0.00)	($0.00)
ST = Premium	$929.52	$1608.26	$1296.25	$1318.94	$687.11	$970.05	$872.77	$786.47	$1340.21	$1054.09	$1086.37
ST = None	$107.85	$106.19	$122.48	$118.40	$111.52	$122.18	$93.38	$72.45	$113.89	$105.08	$107.34
R^2	44.9%	40.5%	48.5%	39.8%	40.2%	43.0%	49.8%	45.0%	46.8%	50.3%	44.9%

ST was a categorical variable that could vary from i) 'None' in case of retention; ii) 'Farm' when buyers purchased on farm or local sale barn; 'NSIP' involving NSIP in the sale; or iv) 'KHSI/Premium sale' for a special sale designation. Because few NSIP sale type observations were available, both NSIP and KHSI/Premium sales were combined into a single 'Premium' category. SEASON was a binary 0/1 variable indicating whether the animal was born in winter (1) or fall (0). WORM was a binary 0/1 variable indicating whether the animal was dewormed prior to sale (1) or not (0). WFEC and EPT were EBV for weaning fecal egg count and ewe productivity trait. Premia and discounts were estimated when the EBV was changed by increasing or decreasing the EBV by one standard deviation (Table 4) + and –, respectively, after the explanatory variable names. The R2 was calculated as $R^2 = 1 - \frac{\sum(P_i - \widehat{P}_i)}{\sum(P_i - \overline{P})}$ where i denotes the ith of 175 observations used for prediction of the individual animal's sale price (P).

allowed recovery from GIN infection due to better nutrition (Coop and Kyriazakis, 1999). Winter-born lambs had a more straightforward increase in FEC by about 120 days of age, as well as lower PCV and higher FAMACHA scores, coinciding with warmer temperatures conducive to *H. contortus* infection. Perhaps because of long-term selection for parasite resistance in the ARS flock, little deworming was needed by 150 days of age and the incidence of deworming did not differ between seasons.

The interaction between season and year on ADG between 60 and 150 days of age, with the highest gains in F19 and W20 lambs, could have been associated with compensatory post-weaning gains. Lower gains in F18 lambs could have been due to lower forage quality, which was not measured in this study, or poor consumption of trace mineralized salt (leading to a change in mineral product in subsequent years). These slower gaining lambs also had lower PCV at 120 days of age relative to the other fall lamb groups. Need for deworming was negatively correlated with ADG, indicating that slower-growing lambs required more deworming and also had more diarrhea. A consistent significance of year × season × lamb age interaction across measured traits suggests that variation among individual year-season classes on lamb performance and GIN resistance was more important than independent effects of birth year and season.

The weaning and post-weaning FEC EBV of sires influenced FEC and PCV of offspring. There was a more rapid increase in FEC of offspring when sire WFEC (both pedigree and genomic) ranged between − 100% and − 70%, suggesting that selection of sires for GIN resistance was most effective among sires with the most extreme favorable EBV (i.e., those with FEC EBV that were closest to −100%). Most lambs were not anemic during the study, but there was an inverse relationship between sire FEC EBV and offspring PCV, suggesting that selection on sire FEC EBV improved both resistance and resilience (the ability to withstand infection) to GIN in the offspring. Indicators of anemia (PCV or FAMACHA) were negatively genetically correlated with FEC and positively correlated with body weight (Bishop, 2012). The relationship between sire FEC EBV and subjective FAMACHA scores was modest in the current study, possibly because most scores were 1 or 2 (n = 3457; not indicative of anemia) and few scores were 3 (n = 236) or 4 (n = 3). No scores of 5 were recorded. Most farmers would not be able to measure anemia except through the use of FAMACHA scores. According to Riley and Van Wyk, 2009, FAMACHA is a heritable trait (0.24) under peak worm challenge. Use of FAMACHA as a selection tool may be useful in flocks that have not begun selection for GIN resistance and those with predominantly *H. contortus*. The scores are not useful in detecting infections involving other GIN genera.

Influences of sire FEC EBV on body weight and ADG were mixed. There was no effect on ADG before weaning, but a positive correlation was detected after weaning, indicating that offspring of the more resistant sires gained less rapidly. On the other hand, there was a negative relationship between sire FEC EBV and body weights when considering all measurements between 60 and 150 days of age, although the difference between offspring of sires with WFEC ranging from − 100% to − 30% WFEC was less than 1 kg. We previously reported a negative but insignificant phenotypic correlation between WFEC and PFEC of the dam and WWT and PWWT of offspring (Notter et al., 2018), confirming that relationships between sire FEC EBV and offspring body weights were minimal. Farmers should consider sires with higher than average WWT and PWWT along with favorable resistance EBV in order to improve offspring growth.

The GEBV were introduced for NSIP Katahdin sheep in October 2021 to increase accuracy of predictions and reduce bias in evaluation of FEC (McMillan et al., 2022). The GEBV were based on an initial reference population of 5000 animals which has continued to grow as more animals are genotyped. Assenza et al. (2014) reported increased accuracy of selection for parasite resistance when pedigree data was combined with genomic data. However, regression equations in Fig. 4 relating $WFEC_P$ or $WFEC_G$ to offspring FEC were similar. Further work on genomics to advance the U.S. sheep industry, including increasing GIN resistance in other breeds, continues (Thorne et al., 2021).

The ewe productivity EBV in Katahdins (Vanimisetti et al., 2007) was designed to assist in the identification and propagation of dams with appropriate prolificacy and adequate milk production in this challenging southern climate. The EPT EBV equation does not include FEC EBV but is still an important consideration in selection and is used for flock improvement by many Katahdin breeders. The EPT EBV significantly influenced the sale value of the animals in the current study. Kelly et al. (2021) likewise found that a maternal index in cattle was positively associated with gross profit.

Sale type had the largest influence on sale price. Premiums for NSIP and or KHSI sales, and rams retained were larger than those associated with farm sales. Second in relative impact was the EPT EBV, suggesting that buyers placed greater emphasis on the EPT EBV than on WFEC. It was unexpected that more desirable/resistant were not valued. Whether the animal was dewormed was tertiary in relative impact, perhaps a more direct and easily understood indicator of resistance to buyers. At the same time, deworming may have been performed as a result of high FEC and as a result, the impact evaluation may have been confounded with WFEC effects. Finally, fall-born lambs were valued less than winter-born lambs, potentially masking their resistance potential and resulting in lower estimated sale prices.

5. Conclusion

It is often said that the sire or ram is half the flock due to his large genetic contribution to offspring and future replacements. Use of sires with NSIP EBV indicating high GIN resistance led to fewer problems in managing GIN in often-vulnerable weaned lambs. However, FEC EBV of ram lambs had little impact on sale price, whereas the ewe productivity trait, which estimates their daughters' maternal productivity was a greater consideration.

CRediT authorship contribution statement

Joan Burke: Conceptualization, Investigation, Methodology, Data curation, Formal analysis, Writing – original draft, Project administration. **James Miller:** Conceptualization, Writing – review & editing, Supervision. **Michael Popp:** Formal analysis, Writing – original draft. **John Anderson:** Formal analysis, Writing – original draft. **David Notter:** Writing – review & editing.

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Declaration of competing interest

The authors report no declarations of interest.

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