Animal 17 (2023) 100772

Contents lists available at ScienceDirect

Animal The international journal of animal biosciences

Breeding options for nematode resistance in Lacaune dairy sheep

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ARTICLE INFO

Article history: Received 14 December 2022 Revised 1 March 2023 Accepted 2 March 2023 Available online 11 March 2023

Keywords: Auxiliary traits FAMACHA© Gastrointestinal nematodes Genetic parameters Parasite resistance

ABSTRACT

Due to progressing anthelmintic resistance of gastrointestinal nematodes (GIN), supportive measures are needed to control these parasites. In sheep, it has been shown that selection towards an increased nematode resistance is feasible and that faecal egg count (FEC) is the generally acknowledged trait for selection. However, a selection based on FEC would come with certain costs, therefore auxiliary, cheaper resistance traits would be most welcome. FAMACHA©, a colour classification of the eyelid, usually used to determine the manifestation of an infection with *Haemonchus contortus*, could serve as such. Therefore, we collected FAMACHA©, packed cell volume (PVC) and FEC phenotypes of approx. 1150 naturally infected Lacaune ewes on 15 commercial farms in Switzerland. The Haemonchus-proportion was determined on farm level. Phenotypic correlations of FEC and FAMACHA© as well as FAMACHA© and PCV were 0.25 (SE 0.03) and -0.35 (SE 0.08), respectively, and correspond well with the results of other studies. A multi-trait animal model was applied to estimate genetic parameters with FEC, FAMACHA©, PVC and milk yield as dependent variables. The heritabilities of FEC, FAMACHA©, PCV and milk yield were estimated to be moderate with values of 0.33 (SE 0.08), 0.30 (SE 0.08), 0.36 (SE 0.08) and 0.34 (SE 0.08), respectively. The genetic correlations between FEC and FAMACHA© and between FEC and PCV were estimated to be close to zero with values of 0.03 (SE 0.22) and 0.01 (SE 0.21), respectively. The average Haemonchus-proportion compared to other GIN was found to be 43%. The FAMACHA© classification of the Lacaune ewes seems to indicate a rather high worm challenge, with 38, 14 and 2% of observations classified to scores 3, 4 and 5, respectively. However, the worm challenge according to FEC was moderate. It has been suggested that the genetic correlation between FAMACHA© and FEC is more pronounced when FEC was high. It could therefore be that the lack of genetic correlation was due to an insufficient worm challenge, even though the Lacaune were grazing at least 70 days before phenotyping. The genetic correlation between FEC and milk yield was estimated to be 0.07 (SE 0.22, slightly unfavourable). We conclude that if FEC is used as trait, the Lacaune could be selected for lower susceptibility towards nematode infection. The use of FAMACHA© as an auxiliary trait for FEC is not feasible, due to an inexistent genetic correlation between these two traits.

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Implications

Parasitic nematodes are a challenge for dairy sheep farming, and the selection of more resistant sheep may help to cope with the situation. We found that the number of nematode eggs per gram faeces was moderately heritable (0.33, SE 0.08), suitable for breeding and associated with a positive but low genetic correlation with milk yield (0.07, SE 0.22). A cheaper and easy-to-obtain trait could be FAMACHA©, a colour classification of the eyelid of sheep. However, we found no genetic correlation between FAMACHA©

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https://doi.org/10.1016/j.animal.2023.100772

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and nematode eggs per gram faeces, rendering FAMACHA© unsuitable as an auxiliary trait in the observed Swiss Lacaune population.

Introduction

The control of infections with gastrointestinal nematodes (**GIN**) in pasture-based sheep production systems is crucial due to associated high production losses (Morgan et al., 2013) and animal welfare issues. Gastrointestinal nematodes have been mainly controlled by the use of anthelmintics for the last decades. However, the available agents are losing efficiency and resistant populations of GIN are now widespread in Europe (Ploeger and Everts, 2018; Rose Vineer et al., 2020; Untersweg et al., 2021). This development will make it difficult for small ruminant farmers to







safely control GIN by the use of anthelmintics. Besides, the loss of effectiveness, the widely used anthelmintic family of the 'macrocyclic lactones' is assumed to be associated with long-lasting negative effects on invertebrates after deposition in the environment (Finch et al., 2020; Sands and Noll, 2022). This is another reason why the reduced use of anthelmintics is appreciated.

One of the possible ways to reduce the dependence on anthelmintics could be the selection of sheep with lower susceptibility to nematode infection (Torres-Acosta and Hoste, 2008; Gilleard et al., 2021), as the mechanisms for resistance towards GIN are genetically determined (Karlsson and Greeff, 2012). In sheep, the number of nematode eggs per gram faeces (FEC) is acknowledged as resistance trait. In two recent meta-analyses, where FEC was used as one of the main parameters for parasite resistance, the global heritability for FEC was estimated to be 0.17 (Medrado et al., 2021) and 0.22 (Hayward, 2022). It has been shown that meat sheep genotypes that were selected for 15 years for low FEC had a significantly lower number of adult nematodes at necropsy and an FEC of only 18% compared to the unselected control (Kemper et al., 2010). This proves that selection for a significantly lower susceptibility to GIN infection is feasible when using FEC as trait. However, little information exists on the nature of genetic correlations between FEC and milk yield (MY) in dairy sheep.

The routine use of FEC in a breeding programme would have the disadvantage of a relatively labour and cost intensive approach (animal sampling and coprological procession). Therefore, cheaper auxiliary traits for parasite resistance would be highly appreciated. The FAMACHA© system has been developed to assign a score to the colouration of the conjunctiva of small ruminants, as a tool to identify animals impacted by Haemonchus contortus infection (van Wyk and Bath, 2002). Haemonchus contortus is a bloodsucking abomasal nematode and infection can cause anaemia which is reflected in the bleaching of the conjunctiva. The scoring is considered cheap and relatively easy to carry out. Decent phenotypic correlations between FAMACHA©, packed cell volume (PCV) and FEC have been reported (Kaplan et al., 2004; Notter et al., 2017), improving with increasing H. contortus proportions (Schwarz et al., 2020). Although reports on phenotypic correlations of FAMACHA© or PCV and FEC are somewhat inconsistent, some authors have reported favourable genetic correlation and a moderate heritability of FAMACHA© (Cloete et al., 2016; Balconi Margues et al., 2020), suggesting that FAMACHA© might be used as an auxiliary trait for the selection of sheep with lower susceptibility towards GIN infection.

Therefore, the objective of this study was to derive the heritabilities and genetic correlations of FEC, FAMACHA©, PCV and MY in a Swiss Lacaune subpopulation based on the estimated variance components.

Material and methods

Study design, farm and animal requirements

Data collection took place from the end of August to mid-December 2019 on 15 commercial Swiss Lacaune dairy sheep farms, of which 14 were certified organic. In order to be considered for the study, the potential animals and farms had to fulfil a number of conditions: (i) pure bred Lacaune animals only, defined as animals with \geq 87.5% Lacaune blood, (ii) at least 30 lactating animals per farm, (iii) daily pasture access per farm for all animals for at least 70 days before sampling date to allow natural infection with gastrointestinal nematodes, (iv) availability of milk performance data, (v) no applied anthelmintic treatment during lactation and grazing period 2019 and (vi) the respective dairy sheep farm had to be a member of the Swiss dairy sheep herdbook, which guarantees known pedigrees of each phenotyped animal. Farm visits were timed so that they were no more than three days away from an official milk recording date.

Faecal egg count, coproculture and H. contortus identification

Procedures for FEC, coprocultures and *H. contortus* identification were done as described in Schwarz et al. (2020). In brief, animals were sampled individually and faecal samples were taken directly from the rectum and stored at 6 °C until processing them until no later than four days with a modified McMaster technique. At each farm visit, 10–25 random animals, depending on farm size (approx. 10% of total stock), were additionally sampled and pooled in two to five jars with a volume of 250 ml each, to obtain third-stage larvae from coproculture after incubation at 25 °C and 80% humidity for 10–14 days. From each jar, 100 third-stage larvae were differentiated according to keys provided by Deplazes et al. (2013) and van Wyk et al. (2004) to determine the proportion of *H. contortus* compared to all other third-stage GIN larvae.

Packed cell volume and FAMACHA© score

Blood samples were taken by jugular vein puncture in 2-ml EDTA vacutainer tubes and stored cool at 5 °C until processing within 24 hours, using a microhematocrit method. To do so, samples were allowed to adjust to room temperature for one hour, then, the blood was filled into microhematocrit tubes and centrifuged at 9 600g for five min (Heraeus Pico 17). The FAMACHA© score was obtained by using the FAMACHA© card to classify the animals to a score from one to five as described by van Wyk and Bath (2002). FAMACHA© was measured by three persons. A possible observer effect was not realised, as mostly two observers worked parallel or rotational on the same farm at a phenotyping event. In case of uncertainty how to score an animal, the decision was made in consultation of the second person. Packed cell volume was included as control for the accuracy of FAMACHA©. FAMA-CHA© is considered accurate if the correlation coefficient is significant and comparable to values found in literature.

Statistical analysis

Descriptive statistics and data preparation for variance component estimation were performed using R (R Core Team, 2022). A total of 1208 animals with phenotypic data were available on the 15 farms. Of these, 21 were rams. Although the rams were phenotyped, they were excluded from the estimation of genetic parameters due to different management compared to females and small numbers. Variance components and breeding value (**EBV**) estimations as well as the preceding pedigree preparation and renumbering were performed with programs from the BLUPF90 package (Misztal et al., 2022). A multi-trait animal model with fixed and random effects was applied. The model for the analysis was built following Heckendorn et al. (2017):

$$y_{ijklmno} = herd_i + month_j + lac_k + dimcl_1 + heamcl_m + a_n + e_{ijklmno}$$
(1)

where $y_{ijklmno}$ is the trait of interest of animal n in herd i, with phenotyping month j, in lac k, in dimcl l and with haemcl m. Herd_i is the fixed effect of herd, month_j the fixed effect of the phenotyping month, lac_k the fixed effect of the lactation, dimcl_l the fixed effect of the days in milk class, heamcl_m the fixed effect of the average *H. contortus* class of the herd, a_n the random animal effect and e_{ijklmno} the random residual effect. All traits of interest, namely FEC, FAMACHA©, PCV and MY, were evaluated with the same fixed and random effects.

In order to achieve an approximation of a normal distribution for FEC, the untransformed trait was converted with a Box-Cox transformation (Box and Cox, 1964) applying the following formulas and a prior computed $\lambda = -0.464$.

$$FEC_{100} = FEC + 100$$
 (2)

$$FEC_{100,rans} = (FEC100^{\lambda} - 1)/\lambda$$
(3)

Prior to the transformation, FEC phenotypes >20 000 were set to 20 000. All values of the categorial trait FAMACHA© which were not 1, 2, 3, 4 or 5 were set to missing. The PCV values had to be in the range of 15–45, otherwise, the outlier was replaced by a missing value code. The plausibility check for MY (result for the test day closest to the day of worm phenotyping) was carried out with respect to the actual lactation stage of the ewes. All test day results were assessed as plausible and ranged from 0.1 to 4.5 kg/day. The assessment was made by comparing the MY results of this subpopulation with the official test day results of the entire Swiss Lacaune dairy sheep population from 2018 to 2020.

All fixed and random effects had to be present, and they were checked or categorised as follows: Each phenotypic record had to be assignable to a herd number ranging from one to 15. The phenotyping period has taken place from August to December. Samples taken from August to October were given a value of one, and samples taken later than October were given a value of two. Days in milk (**DIM**) was categorised as follows: DIM < 100, class one; DIM > 100 and DIM < 150, class two; DIM > 150 and DIM < 200, class three; DIM > 200, class four. The lactation numbers 1, 2 and 3 were handled separately as three groups, and from the fourth lactation onwards, all were assigned to group four. In addition, the herds were divided into three groups according to average H. con*tortus* infestation: Haemonchus-infestation \leq 30, class one; Haemonchus-infestation > 30 and Haemonchus-infestation < 60, class two; Haemonchus-infestation > 60, class three. It was verified that each animal ID was registered in the official pedigree of the breeding organisation and that each phenotype sample had a complete set of effects. After applying all preconditions, 1109 ewes with phenotypic records were available for genetic analysis. These ewes descended from 89 different sires and 809 different dams. The size of the pedigree was in total 2712 animals.

In order to avoid numerical problems in the variance component estimation FEC_{100_trans} , FAMACHA© and MY were multiplied by 1000, PCV by 100. The variance component estimation was conducted with AIREMLF90 (Misztal et al., 2022) after passing 100 rounds in REMLF90 (Misztal et al., 2022). Heritabilities and genetic correlations (r_g) between the traits of interest were computed with AIREMLF90 (Misztal et al., 2022) applying the appropriate options. Subsequently, EBV were estimated with BLUPF90+ from the software package mentioned above.

Results

Phenotypic key figures

The total number of alive Lacaune ewes in lactation registered in the Swiss herdbook is 4 589 (database query December 2022). Of these, 1 187 animals with phenotypic data were available on 15 farms. Additionally, 21 rams were phenotyped. Mean, median and SD of the traits of interest are shown in Table 1. Not all animals had measurements for all phenotypes; therefore, the number of observations per herd is partly different. Mean value of FEC over all animals was 875 ± 2 347; rams presented a higher FEC value with 1 748 \pm 3 206 than ewes with 858 \pm 2 327. Faecal egg count median for female and male animals was 150 and 450, respectively. The mean FAMACHA© score was 2.67 ± 0.89 and differed between ewes (2.68 ± 0.89) and rams (2.33 ± 0.90) . There was also a difference in PCV between ewes (31.11 ± 3.99) and rams (33.88 \pm 2.80). Milk yield for the test day closest to the day of worm phenotyping was 1.4 ± 0.7 kg milk/d. Thereby, the ewes were on average 191 ± 74 DIM. At the time of phenotyping, 26.6% of the ewes were in their first lactation, 17.2% in their second, 19.5% in their third, and the remaining ewes (36.7%) in their fourth or higher lactation.

The comparisons between the phenotyped herds can be found in Table 1. The mean FEC varied between herds (123–4 851). With the exception of herd 1 with a mean FEC of 4 851, all herds were in an FEC range between 123 and 719. The medians were lower for all herds, which is an indicator of a skewed distribution. The mean FAMACHA© score per herd ranged from 2 to 3.2, and the medians were also in the same range. The herd averages of PCV were found between 29.4 and 35.7. Except for herd 7 with a mean PCV of 35.7,

Table 1

Descriptive characterisation of Faecal egg count (FEC), FAMACHA®, Packed cell volume (PCV) and milk yield in dairy sheep for each herd contributing phenotypes.

Herd		Trait															
		FEC			FAMACHA©			PCV			Milk yield						
	Sex	n	Mean	Median	SD	n	Mean	Median	SD	n	Mean	Median	SD	n	Mean	Median	SD
1	Female	134	4 851	3 500	4 962	138	3.1	3.0	1.0	139	30.1	30	5.8	140	1.6	1.6	0.6
2	Female	72	123	50	193	72	2.9	3.0	1.0	73	33.1	33	2.7	73	1.1	1.0	0.3
3	Female	85	163	100	239	84	3.0	3.0	0.7	85	31.0	31	3.2	85	1.1	1.0	0.3
4	Female	16	197	25	281	17	3.2	3.0	1.1	17	26.3	26	2.2	17	1.2	1.2	0.3
5	Female	208	208	50	653	213	2.6	3.0	0.7	210	29.1	29	2.9	213	1.1	1.0	0.4
6	Female	52	150	75	197	54	2.8	3.0	0.8	54	31.7	32	4.1	54	1.6	1.6	0.5
7	Female	72	427	0	1 755	75	2.1	3.0	0.5	74	35.7	36	3.9	75	1.2	1.2	0.5
8	Female	33	233	100	450	35	2.8	3.0	0.9	35	31.8	32	2.3	35	1.0	1.0	0.3
9	Female	30	472	425	370	33	2.9	3.0	0.6	33	30.9	32	2.2	33	0.9	1.0	0.3
10	Female	64	315	200	485	66	3.0	3.0	0.7	66	33.2	33	2.6	66	1.0	1.0	0.3
11	Female	64	144	50	306	69	3.0	3.0	0.9	69	30.5	30	3.4	69	1.3	1.2	0.5
12	Female	58	719	550	742	61	2.6	3.0	0.6	61	29.4	29	3.1	61	1.2	1.0	0.6
13	Female	177	476	150	795	177	2.0	2.0	0.8	174	32.1	32	3.3	178	1.5	1.2	1.0
14	Female	41	602	550	353	42	2.8	3.0	0.9	42	30.7	31	3.0	42	2.7	2.5	0.7
15	Female	46	642	475	550	46	2.9	3.0	0.8	46	30.6	30	3.4	46	2.4	2.5	0.5
All	Female/male	1 173	875	150	2 347	1 197	2.7	3.0	0.9	1 195	31.2	31	4.0	1 187	1.4	1.2	0.7
All	Male	21	1 747	450	3 206	15	2.3	2.0	0.9	17	33.9	34	2.8	-	-	-	-
All	Female	1 152	858	150	2 327	1 182	2.7	3.0	0.9	1 178	31.1	31	4.0	1 187	1.4	1.2	0.7
Genetic analysis	Female	1 109	876	150	2 365	1 104	2.7	3.0	0.9	1 101	31.1	31	4.0	1 109	1.4	1.2	0.7

Table 2

Phenotypic (lower triangular) and genetic correlations (upper triangular) between Faecal egg count (FEC), FAMACHA©, Packed cell volume (PCV) and milk yield in dairy sheep. Heritabilities are on the diagonal, SE are in brackets. Phenotypic correlations were calculated with untransformed FEC. Genotypic correlations are based on transformed data (FEC_{100_trans}).

Trait/Trait	FEC	FAMACHA	PCV	Milk yield
FEC	0.33 (0.08)	0.03 (0.22)	0.01 (0.21)	0.07 (0.22)
FAMACHA	0.25 (0.03)	0.30 (0.08)	-0.47 (0.19)	0.23 (0.21)
PCV	-0.36 (0.03)	-0.35 (0.08)	0.36 (0.08)	-0.11 (0.20)
Milk yield	0.16 (0.03)	0.07 (0.03)	-0.20 (0.03)	0.34 (0.08)

all other herds were close together. The herd average of daily MY scattered more. The lowest mean was 0.9 kg/day (herd 9), and the highest was 2.4 kg/d (herd 15).

Phenotypic correlations (r_p) between the traits of interest can be found in Table 2. All are in a very low to moderate positive or negative range between -0.36 and 0.25. The phenotypic as well as the genetic correlation between FEC/FEC_{100_trans} and FAMA-CHA© are of particular interest. We computed r_p = 0.25 between these two traits and more detail, especially the distribution of the number of observations on the individual scores can be seen in Fig. 1.

Variance components and genetic parameters

The estimated variance components as well as the heritabilities can be found in Table 3. All heritabilities are in a favourable medium range indicating that breeding efforts are possible. Genetic correlations between the traits of interest (Table 2) are between -0.47 (PCV, FAMACHA©) and 0.23 (MY, FAMACHA©). Genetic correlation (FAMACHA/FEC100_trans), r_g (PCV/FEC100_trans) and r_g (MY, FEC100_trans) are almost 0. Genetic correlation between our main trait (FEC100_trans) and the targeted auxiliary trait FAMACHA© is 0.03.



Fig. 1. Violin plot of Faecal egg count (FEC) and FAMACHA© in dairy sheep including the number of observations for each score. The median and the mean are indicated by a blue dot and a green triangle, respectively.

Unfortunately, we found a weak r_g between FEC_{100_trans} and MY. However, it is evident from Fig. 2 that there are animals in our phenotyped subpopulation that have favourable EBV at FEC_{100_trans} as well as at MY.

Discussion

Heritabilities

The estimated heritability of FEC_{100_trans} in our study was at the upper end of the usually reported scale and exceeded the global estimates pointed out in the recent meta-analyses being 0.17 (Medrado et al., 2021) and 0.22 (Hayward, 2022). However, recent studies on the heritability of FEC in dairy sheep did report also heritabilities above 0.3 (Aguerre et al., 2018; 2022). The rather high heritability of FEC_{100_trans} in our study could be partly due to the rather small subpopulation of nearly 1 200 animals only. This may contribute to slight deviations from the estimates reported in the two recent meta-analyses. It also seems that the sex of the phenotyped animals can have an effect on the estimated heritability, with observations concerning females only, as is the case in our study, yielding higher heritabilities (Hayward, 2022). Even though the heritability of FEC_{100_trans} would be slightly overestimated in our work, it would in any case allow a selection of the Lacaune for a lower susceptibility towards GIN infection. The implementation of a breeding strategy based on FEC_{100_trans} would be feasible but would come with a certain amount of costs for sampling and coproculture analysis. Therefore, we also recorded the FAMACHA© score and heritability was estimated to be 0.30. This estimate is at the upper end, but within the confidence intervals estimated by the two recent meta-analyses on the genetic parameters of sheep (Medrado et al., 2021; Hayward, 2022).

FAMACHA© and its correlation to Faecal egg count

Our observed phenotypic correlations of FAMACHA© and PCV are within the usually reported range (Burke et al., 2007; Kaplan et al., 2004; Moors and Gauly, 2009) and the correlation coefficient of FAMACHA© and PCV was significant, therefore, we assume an adequate recording of FAMACHA©. As four of the 15 farms had a *Haemonchus*-proportion below 20%, we decided to include this information in the model for the estimation of genetic parameters,

Table 3

Estimated variance components and heritabilities (SE in brackets) for the traits of interest in dairy sheep.

Trait	Additive genetic variance	Residual variance	Phenotypic variance	Heritability
Faecal egg count _{100_trans} ¹	1 055	2 133	3 188	0.33
	(286)	(225)		(0.08)
FAMACHA©	192 060	456 480	648 540	0.30
	(56 056)	(45 496)		(0.08)
Packed cell volume	42 439	74 808	117 247	0.36
	(10 796)	(8 345)		(0.08)
Milk yield	70 210	137 670	207 880	0.34
-	(18 551)	(14 584)		(0.08)

¹ FEC_{100_trans} = (FEC100^{λ} - 1)/ λ , where λ = -0.464.



Fig. 2. Scatter plot of estimated breeding values (EBV) of transformed Faecal egg count (FEC100_trans) and milk yield in dairy sheep. Animals with estimated breeding values above average and FEC100_trans below average (suitable for selection) are indicated by red dots (quarter down right).

since the sensitivity of FAMACHA© depends on the presence of this hematophagous nematode. Nevertheless, the rg of FEC_{100 trans} and FAMACHA© was estimated to be close to zero in our study. A low r_g (0.17) of FEC and FAMACHA© was also estimated by Rodrigues et al. (2021) in a herd of Santa Inês sheep. In contrast, Balconi Marques et al. (2020) have found a moderate-to-high rg (0.55) of FAMACHA© and FEC in Corriedale meat lambs. Cloete et al. (2016) found contradictory results when estimating the r_g and FAMACHA© FEC in two farm of populations (Dormer \times Merino lambs and Merino hoggets): a high positive correlation (0.66) on one farm but a moderate negative r_g (-0.29) on the other.

It seems that rg of FAMACHA© and FEC does not only depend on the Haemonchus-proportion but also on the intensity of the worm challenge. Riley and Van Wyk (2009) found a higher r_g between FAMACHA© and FEC when the worm challenge peaked (0.32) but no linkage when the worm challenge was low (0.01). These authors defined a period with high worm challenge as a period when mass treatments were necessary, e.g. all animals judged to the FAMA-CHA© categories three to five were drenched. According to this, 53% of the Lacaune ewes in this study would have been classified as animals with high worm challenge. In the work of Balconi Margues et al. (2020), in which a moderate-to-high r_g of FEC and FAMACHA© was estimated, only 29% of the observations were classified FAMACHA© three or higher. The comparison of the FAMACHA© classifications in our work with the two beforementioned studies does not suggest that the worm challenge was particularly low in our observed population. When comparing the FEC level, however, the lambs in both aforementioned studies showed a higher egg excretion. The observations in our study took place late in lactation and lactation peak was passed, suggesting that immune functions were prioritised over milk production again (Houdijk et al., 2003). It could be that this improved immune response against GIN resulted in moderate FEC levels. Eventually, the worm challenge was not high enough to yield a significant genetic correlation of FEC_{100_trans} and <code>FAMACHA</code>©, analogous to the group of lambs with low worm challenge in the work of Riley and Van Wyk (2009). On the other hand, FEC was not particularly low either, with a mean FEC of 745, 1 957 and 4 294 in animals that scored FAMACHA© three, four and five, respectively. The decision to phenotype only animals after lactation day 70 has been set with the intention to allow a sufficient contact with GIN on pasture, after drenching of the ewes in the dry period. This period considers also the use of products with longer-lasting impact as well as the subsequent prepatency period. Sampling earlier in lactation might have resulted in more animals with higher worm challenge.

But the risk of false-negative animal assessments due to the lasting impact of anthelmintic use would have increased.

FAMACHA© was evaluated as a possible auxiliary trait for FEC to select animals quicker and cheaper for improved resistance towards GIN infection. However, the results of this study do not recommend FAMACHA© as an auxiliary trait in this context, due to the non-existent genetic correlation with FEC. The use of FAMA-CHA© as an auxiliary trait would, according to the results of this study, not improve animal resistance towards GIN infection. The rejection of FAMACHA© as an auxiliary trait leads to the conclusion that selection would have to be based on FEC. Kemper et al. (2010) showed that a selection with a focus on low FEC led to significantly improved GIN resistance within 15 years. However, applying a breeding strategy with a total merit index that reflects the overall breeding goal, other traits need to be considered as well and it would take longer to reach comparable achievements regarding GIN resistance.

The possible dependence of FAMACHA© on the infection pressure as well as on Haemonchus prevalence reduces the attractiveness and feasibility as a potential auxiliary trait for improved GIN resistance. However, this reasoning does not rule out the possibility of FAMACHA© having a function as a resilience trait.

Genetic correlation of faecal egg count and milk yield

The estimate for the heritability of MY in our study was moderate and slightly higher than usually reported (Carta et al., 2009). The genetic correlation of MY and FEC_{100_trans} was positive (e.g. unfavourable), but low. Aguerre et al. (2022) even found moderate positive correlations of FEC and MY, supporting our estimates that selection for a low FEC might at the same time select for lower a MY. On the other hand, Hayward (2022) concluded that a selection for improved resistance towards GIN, contrary to popular belief, is not necessarily unfavourably correlated with performance traits. In fact, he estimated a low but favourable correlation between FEC and performance traits. However, few dairy sheep data were included in that meta-analysis. Generally, the mean day of lactation being day 191 was late in our study. Beyond the possible impact on the relationship between FAMACHA© and FEC_{100 trans}, this may also have had an impact on the genetic correlation between FEC_{100_trans} and MY. Phenotyping in an earlier stage might have yielded different genetic correlations, which has to be considered when interpreting our data.

Other genetic correlations

A positive and moderate genetic correlation of FAMACHA© and MY suggests that a hypothetical selection of animals with desired low FAMACHA© scores would be accompanied by a loss of milk performance if MY is not considered with appropriate weight in a potential selection scheme. Packed cell volume has mainly been included to serve as a control for FAMACHA© but was also included in the variance component estimation. Comparable to FAMACHA©, a non-existent genetic correlation of PCV and FEC was estimated, rendering PCV unsuitable as an auxiliary resistance trait for the observed subpopulation. The time required for blood or faeces collection in the field should be comparable. The subsequent work in the laboratory, however, would be much faster for PCV. From this perspective, PCV would be preferable in terms of cost. However, it is unlikely to assume that farmers will be allowed to take blood without further ado, as this work is likely to be restricted to veterinarians. Contracting veterinarians for blood sampling should at least offset the cost savings of PCV in the laboratory due to the higher costs of blood sampling. Due to the abovementioned reasons, PCV seems not very promising to serve as (cheaper) auxiliary trait for FEC.

Conclusion

We conclude that a selection for lower susceptibility towards GIN infection in the studied Swiss Lacaune subpopulation would be possible when using FEC as a trait. Even though there was an unfavourable but low genetic correlation of FEC and MY, a selection should be possible due to a nevertheless considerable share of animals with low EBV of FEC_{100_trans} and above average MY at the same time. A non-existent genetic correlation of FAMACHA© and FEC_{100_trans} suggests that the use of FAMACHA© as an auxiliary trait will not be feasible, as this will not lead to a selection response in FEC considering the results of the subpopulation studied here. Additional data, especially considering more animals in an earlier lactation stage with repeated measurements, might yield different results.

Ethics approval

Animal-related procedures followed the Swiss animal welfare act, the animal welfare ordinance as well as the animal experimentation ordinance with approval from the veterinary offices of the involved Cantons of Switzerland, permission No. 75730.

Data and model availability statement

None of the data were deposited in an official repository. Pedigree data are owned by the 'Swiss Dairy Sheep Breeders Cooperative' and are not available. Parasitological data are presented in this work.

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Declaration of interest

None.

Acknowledgements

We thank all dairy sheep farmers who participated in the study. We also would like to thank the Swiss Dairy Sheep Farming Cooperative for the provision of milk recording results and pedigree information. We are grateful for the help of S. Dörig and T. Manser from the Swiss Advisory and Health Service for Small Ruminants. The Swiss Advisory and Health Service for Small Ruminants is the official distributor of FAMACHA© cards in Switzerland, and we would like to thank them for the allowance to use the FAMACHA©-cards.

Financial support statement

This work has received funding from the European Union's Horizon 2020 research and innovation programme under Grant Agreement No 772787 (SMARTER).

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