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Studies of inheritance of resistance to *Haemonchus contortus* through diallel mating in Garole sheep

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Abstract
45 male and 58 female Garole sheep were divided into resistant, susceptible and highly susceptible groups to natural infection of *Haemonchus contortus* based on faecal egg count and subsequently Diallel mating was applied in two subsequent generations to study the inheritance and variability of resistance. A total of 505 lambs were examined for faecal egg count at 3rd, 6th and 8th months of age. The overall resistance had been increased after Diallel mating in second and third generations as compared to parent generation. In both generations, lambs produced from resistant parents had significantly lower EPG. Highest and lowest EPG was recorded at 3rd and 8th month of age respectively. A high heritability of EPG was estimated in lambs of all ages in second and third generation at 3rd, 6th and 8th months of age. A moderate to high repeatability was estimated for EPG in first, second and third generation. Results of this study indicate heritable variations of resistance to *Haemonchus contortus* in Garole sheep. Thus, selection of rams and ewes can be made as early as six months of age.

Keywords: Garole sheep, *Haemonchus contortus,* EPG, resistance, diallel mating, heritability, repeatability

1. Introduction

Gastrointestinal (GI) nematodes are often one of the most important hindrances to the successful raising of small ruminants (American Association of Veterinary Parasitology, 1983). Apart from the use of modern anthelmintics some other factors have arisen recently that epitomize that to depend on the drugs as a sole means of parasite control is a serious mistake.

In small ruminants, parasites have developed resistance against all classes of anthelmintics currently employed, and resistance to multiple classes of drugs by the same parasite in common place [26, 33, 35]. A second concern about this dependence on anthelmintics is the growing insistence of consumers that their food and environment be free of chemical residues [18].

Resistant to diseases in general, and to parasitic diseases in particular, is a genetically variable characteristic of all animals, including domestic species [15]. It may not be possible, or even desirable, to identify animals which have complete genetic resistance to nematode infection, but there is considerable evidence that part of the natural variation in resistance in under genetic control [4, 16, 29, 32].

The saline belt of Sunderban Delta of South 24 Parganas, some parts of North 24 Parganas and some saline zone of Purba Midnapur district of West Bengal, India, is the main habitat of Garole sheep. The climate is hot and humid. These sheep are indigenous and is popular for its biannual lambing with multiple births and their ability to graze on aquatic weeds and grasses standing in knee-deep water for hours together [19] without being affected by foot rot diseases [22].

Most of the genera of parasites found in ruminants stimulate a relatively effective level of immunity in most animals after several months on pasture. This immunity significantly reduces the number of worms that become established in the grazing animals; the exception to this is *Haemonchus contortus* in sheep. In sheep, lambs under the age of about 8 months do not develop significant protective immune responses to infection or immunization [30]. This prolonged susceptibility to reinfection is a major reason why this parasite remains the most economically important GI nematode in sheep.

Faecal egg counts have been shown to have moderate (0.61) to high (0.91) correlation with nematode burdens [3, 28], and in essence might be considered a direct measure of infection.

Resistance to *Haemonchus contortus*, as measured by faecal egg count (FEC), has moderate heritability (0.22 to 0.43) indicating that selection and breeding of sheep for increased resistance is possible [1, 6, 8, 36], but research in this line is limited in India and particularly it is very few for Garole sheep. Genetic parameters for resistance are also not available for *Haemonchus contortus* infections in Garole sheep although infections exist and are widespread.

Most research pertaining to the genetics of resistance to internal parasites in sheep has been conducted in Australia and New Zealand and to some extent in United Kingdom [6, 7]; but the research in this line is limited in India and particularly it is absent for Garole sheep. Realizing the importance of the subject, a research programme was taken up in Garole sheep to study the inheritance and obtain the genetic parameters for resistance to *Haemonchus contortus* infection and to produce a genetically superior stock as an adjunct to current methods of GI parasite control.

2. Materials and Methods

2.1 Site of experiment

This experiment was conducted in Garole sheep (*Ovis aries)* during the period of December'2001 to December'2004, maintained in a farm of West Bengal University of Animal and Fishery Sciences, Mohanpur Campus, Nadia, West Bengal, India, Under National Agricultural Technology project on "Animal Genetic Resource Biodiversity". The farm is situated at $88^0 32'$E Longitude and $22^0 56'$N Latitude with an altitude of 9.75 mt above mean sea level having humid climate. During the experiment period temperature varied within the range of 7.27ºC to 39.98ºC and relative humidity varied from 47.18% to 97.69%.

2.2 Experimental animal

The experiment was started with a parent stock of 103 sheep (45 male and 58 female). Out of these 58 ewes and 32 rams were used for selective breeding to produce second-generation offsprings. In the second-generation, out of 106 adult sheep (produced by Diallel mating), 50 ewes and 11 rams were mated selectively to produce third generation lambs. During the experimental period a total of 505 lambs were born of which 404 were of the second generation and 101 were of the third generation.

2.3 General managemental practices of animals

All the experimental animals were allowed for grazing on natural pasture from 8 A.M. to 3 P.M. in winter months (November to February). During summer (March to June) and monsoon (July to October) animals were grazed in two shifts viz. from 7 A.M. to 10.30 A.M. and 2.30 P.M. to 5.30 P.M. The pasture comprised mainly of doob grass (*Cynodon dactylon*) with other grasses and leaves viz. goose grass (*Eleusine indica*), horse purseane (*Trianthema monogyna*) and anjan grass (*Cenchrus ciliaris*). In addition to grazing all the animals were offered about 50g concentrates after returning from grazing in the evening. *Adlibitum* water was provided to all the animals in all seasons.

The animals were housed in groups during the night in sheds. They were provided with floor space as per B.I.S. Routine vaccinations against endemic diseases of this location were carried out. Animals were clinically checked routinely and dewormed by Fenbendazole or Albendazole and Rafoxanide @7.5 mg to 10 mg/kg body weight orally for 3 times in a year and dewormed regularly viz. ewes and rams were dewormed for 3 times in a year where as lambs were dewormed first at 2 months age and then at monthly intervals. Animal's sheds were cleaned every day. Animals were given dips from time to time to protect them from ectoparasites.

2.4 Experimental design

As sheep were maintained in a common natural pasture throughout the year, it was assumed that they got an equal dose of *Haemonchus contortus* infection from the grazing field. All the sheep were evaluated for their parasitic load. Sheep were grouped into resistant, less susceptible and highly susceptible to *Haemonchus contortus* on the basis of eggs per gram of faeces (EPG) that is presented in Table-1. Animals with EPG up to 600, above 600 up to 1200 and above 1200 were considered as resistant, less susceptible and highly susceptible respectively (Table-1).

Table 1: Groups of sheep according to parasitic load

Status	Group	Parasitic load (EPG)
Resistant	I	Up to 600
Less susceptible	II	Above 600 - up to 1200
Highly susceptible	III	Above 1200

A complete 'Diallel mating' was applied where ram of a particular group was allowed to breed with all the ewes for 21 days and then replacing by other ram rotationally (Table-2). This procedure was continued throughout the study period. All the parents and lambs of 3 to 8 months of age were evaluated for their parasitic load and grouped accordingly.

Table 2: Mating type

Mating type	Rams Group	Ewes Group
Type - 1	I	I
Type - 2	I	II
Type - 3	I	II
Type - 4	II	I
Type - 5	II	II
Type - 6	II	III
Type - 7	III	I
Type - 8	III	II
Type - 9	III	III

2.5 Collection of faecal sample and estimation of parasitic load

Faecal samples were collected rectally from each animal after one week of deworming and examined in three different seasons (summer, monsoon and winter). During each season two faecal samples were collected from each animal at five days interval for evaluation of *Haemonchus contortus* eggs. Eggs per gram of faeces (EPG) were determined following Stoll's Dilution Method [27]. A glass bottle graduated at 56 and 60 ml was used. The bottle was filled to the 56 ml mark with decinormal caustic soda solution and faeces were added until the fluid reaches the 60 ml mark. The 0.15 ml of the well-mixed suspension was drawn off with a pipette graduated to show this amount and placed on a slide and observed under microscope (10X). The total number of eggs in the 0.15 ml sample was then counted and that number, multiplied by 100, given the number of egg per grams (EPG) of faeces.

2.6 Statistical Analysis

Least-Squares analysis [17] had been performed for lambs of second as well as third generation to study the effects of mating type on EPG at 3rd, ^{6th} and 8th months of age. The model used for analysis was -

$Y_{ij} = \mu + a_i + e_{ij}$

Where, Y_{ij} is the observation on the j^{th} individual in i^{th} mating type.
M = General effect (Overall mean common to all observations)
a_i = Effect of the i^{th} mating type (i=1, 2, 3, 4, 5, 6, 7, 8, 9)
e_{ij} = Random error assumed to be normally distributed with zero mean and variance (σ^2_e).

Duncan's Multiple Range Test [23] was performed to examine the significant differences between means whenever the analysis of variance showed significant differences.

Heritability (h^2) of EPG was estimated following the method of Regression of offspring values on one parent [5].
Repeatability (r) of EPG was determined by the method described by Kempthorne [21].

3. Results and Discussions

Resistance to diseases is a threshold character and does not follow Mendelian inheritance, not it is inherited as quantitative traits [13] and thereby "Diallel mating" system has been adopted for three different lines of sheep (both rams line and ewes line) as well as their progenies to evaluate the favourable mating types to increase the resistance status against *Haemonchus contortus* in the Garole population.

Table 3: Mating type wise Least Squares means of EPG of second-generation lambs

Effects	Age of kids and Mean EPG ± SE		
	3rd month	6th month	8th month
Overall	949.26 ± 7.88 (239)	869.86 ± 7.60 (230)	845.37 ± 9.21 (219)
Mating type:			
Type-1	576.92 ± 29.69^g (13)	558.33 ± 29.31^g (12)	487.50 ± 34.77^g (12)
Type-2	701.25 ± 16.92^f (40)	644.59 ± 16.69^f (37)	610.29 ± 20.66^f (34)
Type-3	820.00 ± 27.64^e (15)	760.00 ± 26.22^e (15)	696.15 ± 33.41^e(13)
Type-4	853.45 ± 19.88^e (29)	750.00 ± 19.19^e (28)	705.56 ± 23.18^e (27)
Type-5	925.40 ± 13.49^d (63)	855.74 ± 13.00^d (61)	846.55 ± 15.82^d (58)
Type-6	1052.27 ± 22.82^c (22)	926.19 ± 22.16^c (21)	931.58 ± 27.63^c (19)
Type-7	1116.67 ± 30.90^c (12)	1045.83 ± 29.31^b (12)	987.50 ± 34.77^c (12)
Type-8	1200.00 ± 20.99^b (26)	1076.92±19.91^b (26)	1090.38 ± 23.62^b (26)
Type-9	1297.37 ± 24.56^a (19)	1211.11 ± 23.93^a (18)	1252.78 ± 28.39^a (18)

Means under different mating type in a column having different superscripts differed significantly. Figures in the parentheses indicate the number of lambs.
The overall Least Square means of EPG were decreases with increase of age (Table-3 & 4); highest at 3rd month of age (949.26 ± 7.88 vs 880.79 ± 22.09), medium at 6th month of age (869.86 ± 7.60 vs 763.42 ± 17.72) and lowest at 8th month of age (845.37 ± 9.21 vs 661.89 ± 15.30) in both the generations which was presented in Table-3 & 4. Effect of mating type on EPG count was found to be highly significant ($P < 0.01$) at all ages in second as well as in third generation lambs. In the second generation, EPG count was highest in Mating Type-9 lambs (1297.37 ± 24.56, 1211.11 ± 23.93 & 1252.78 ± 28.39) at 3rd, 6th and 8th month of age and lowest value was recorded in Mating Type-1 lambs (576.92 ± 29.69, 558.33 ± 29.31 & 487.50 ± 34.77) at all the ages (Table-3).

Differences in EPG count among the lambs of other mating types were recorded in between and found to be non-significant in closure groups in most of the cases (Table-3).
The EPG count in third generation lamb was lowest in lambs of mating type-1 (666.67 ± 68.40, 533.33 ± 54.85 & 550.00 ± 47.36) and highest EPG was recorded in lambs of mating type-8 (1137.50 ± 59.24, 937.50 ± 47.50 & 900.00 ± 45.55) at 3rd, 6th and 8th month of age (Table-4). Differences in EPG count among the lambs of mating type-2, 3 and 5; as well as mating type-1 and 4 were found to be non-significant at 3rd month of age. At 6th month of age no significant differences of EPG count in lambs of mating type-2, 4 and 5; as well as mating type-3 and 8 were noticed. But at 8th months of age, differences of EPG count in lambs of mating type-3, 5 and 8; as well as mating type-1, 4 and 2 were found to be non-significant (Table-4).

Table 4: Mating type wise Least Squares means of EPG of third-generation lambs

Effect	Age of kids and Mean EPG ± SE		
	3rd month	6th month	8th month
Overall	880.79 ± 22.09 (62)	763.42 ± 17.72 (62)	661.89 ± 15.30 (62)
Mating type:			
Type-1	666.67 ± 68.40^d (3)	533.33 ± 54.85^c (3)	550.00 ± 47.36^c (3)
Type-2	885.71 ± 44.78^{bc} (7)	707.14 ± 35.91^b (7)	614.29 ± 31.01^{bc} (7)
Type-3	933.33 ± 68.40^b (3)	933.33 ± 54.85^a (3)	733.33 ± 47.36^a (3)
Type-4	733.33 ± 48.37^{cd} (6)	683.33 ± 38.78^b (6)	533.33 ± 33.49^c (6)
Type-5	928.21 ± 18.97^b (39)	785.90 ± 15.21^b (39)	715.38 ± 13.14^{ab} (39)
Type-8	1137.50 ± 59.24^a (4)	937.50 ± 47.50^a (4)	825.00 ± 41.02^a (4)

Means under different mating type in a column having different superscripts differed significantly. Figures in the parentheses indicate the number of lambs.
These trends indicate that the EPG of lambs of different mating type varied according to the resistance status of their parents against *Haemonchus contortus* infection. These findings may be compared with the findings of Windon and Dineen [34] who reported a significant effect of sire on FEC of progenies (Progeny of resistance sires had lower FEC compared to progeny of susceptible sires against *T. colubriformis*).
Our study also revealed that younger lambs were less resistance to natural infection than that of older lambs. The findings of other scientists [11, 14, 20, 31] were also in agreement with our results, who reported significantly higher egg count in younger lambs as compared to older lambs.

Table-5 depicts that the overall rate of infection decreased in the population and it was significantly lower (P<0.01) in second (863.359±16.747) and third generation (873.350±27.688) compared to first generation (927.538±14.300) after Diallel mating.

Table 5: Least squares means of EPG of adult sheep in different generations

Effects	Number	Mean EPG ± SE
Overall	232	888.082±14.567
Generation:		
First	103	927.538±14.300^{a}
Second	106	863.359±16.747^{b}
Third	23	873.350±27.688^{b}

Means under a particular effect in a column having different superscripts differed significantly.

Heritability of faecal egg count (EPG) in second and third generation lambs at 3rd, 6th and 8th month of age had been estimated and were recorded as 0.610±0.103 vs 0.696±0.152, 0.538±0.094 vs 0.731±0.60 and 0.615±0.107 vs 0.579±0.173 respectively (Table-6). The present estimates of heritability for faecal egg count (EPG) of lambs in both generations were higher than the values reported by different workers [1, 7, 10, 31, 37] who reported heritability estimates for FEC nearer to 0.3 ± 0.1. Woolaston and Piper [36] have reported a heritability of 0.23 for FEC in case of an artificial *Haemonchus contortus* infection in 5 to 6 months old Merino lambs. Morris *et al* [24] reported heritability for individual FEC to range from 0.29 to 0.42 in Romneys facing natural mixed challenges on pasture, with the highest heritability recorded at 7 to 8 months of age. In, the current study, heritabilities of faecal egg count (EPG) were also highest (0.651 ± 0.107) at 8 months of age than all other ages studied.

Table 6: Heritabilities (h^2± SE) of EPG of lambs at different ages

Generation	Age of kids and h^2 ± SE		
	3rd month	6th month	8th month
Second generation	0.610±0.103	0.538±0.094	0.651±0.107
Third generation	0.696±0.152	0.731±0.160	0.579±0.173

These high heritability estimates in Garole sheep indicated the presence of considerable amount of additive genetic variance, which may lead to infer that the resistance status to infection of *Haemonchus contortus* may be improved to a considerable extent by applying higher selection pressure in resistant animals through mass selection.

Repeatability measurement at different seasons for the base population as well as second generation and third generation sheep has been carried out. The repeatability (r ±S.E.) of eggs per gram of faeces (EPG) among different seasons in first-generation, second-generation and third-generation adult sheep have been estimated as 0.463±0.003, 0.50±0.003 and 0.260±0.019 respectively (Table-7) which was almost same value of 0.43 obtained by others scientists [31]. Moderate to high repeatability for faecal egg count has also be reported by other scientists [2, 12, 25].

Table 7: Repeatabilities (r ±S.E.) of EPG in adult sheep of different generations

Parameters	Repeatability (r ±S.E.)		
	First generation	Second generation	Third generation
EPG	0.463±0.003	0.501 ±0.003	0.260 ±0.019

The results of the present study (i.e. higher heritability and moderate to high repeatability of EPG) leads to a concept that selection for increased resistance is possible by taking single measurement in a adult sheep with proper breeding strategies.

The response to natural infection of *Haemonchus contortus* in lambs of the second as well as in the third generation were higher in the 3rd month of age in all mating groups, subsequently decreased with the increase of age and lowest in the 8th month of age. The possible explanation may be that younger lambs appear not to be capable of mounting a strong acquired immune response against the natural infection of *Haemonchus contortus* and thus are less resistant. Acquired resistance improves with age. The EPG of lambs in the second as well as the third generation were significantly lowest in mating type-1 and it was moderate in lambs up to mating type-7, although significantly different from each other in most of the cases. Therefore it can be concluded that there is a significant effect of sire as well as a dam on lambs FEC. The progenies of resistant parents were found to have lower FEC as compared to susceptible parents at all ages. EPG of lambs was highly heritable in all the periods in second as well as third generations. The repeatability estimates for EPG were also high in all the generations.

5. Conclusion

From this study it can be concluded that resistance to *Haemonchus contortus* in Garole sheep is existed and heritable. There is an ample scope for increasing the resistance population through selective breeding or assortative mating of resistant animals. Further the response to natural infection of *Haemonchus contortus* may be studied in Garole sheep as early as 6 months of age and selection of breeding animals (i.e. young rams and ewes) can be done accordingly by taking single FEC which will be helpful to develop a resistant population.

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