Research paper

Comparison of the timing of development of immunity in Romney lambs from resistant and resilient selection lines

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ABSTRACT

Variation in the timing of development of immunity to gastro-intestinal nematode parasites was assessed in resistant and resilient Romney selection lines exposed to mixed natural infection. From weaning, at mean 92 days-of-age, animals (n = 53) were sampled for faecal egg count (FEC) expressed as eggs per gram of faeces (epg), saliva for immunoglobulin (IgG and IgA) determination and fasted live weight (LW) every 10 days until 351 days-of-age. Overall, mean back-transformed FEC were consistently low for resistant animals (< 200 epg) whereas resilient counterparts' FEC increased with time to reach a peak of 1400 epg at day 230 for females and 1800 epg for males at day 280 before declining to less than 500 epg by day 300, respectively (P < 0.001). Resistant lambs reached a threshold for *Trichostrongylus colubriformis* L3-specific IgG which was indicative of the presence of immunity earlier at 220.6 ± 8.8 days-of-age compared with resilient-line animals which reach this threshold 40 days later at 263.4 ± 6.9 days-of-age (P < 0.001). In addition, resistant females reached sexual maturity earlier compared with their resilient counterparts *viz.* 263.5 ± 3.7 *c.f.* 274.4 ± 3.4 days-of-age, respectively, (P = 0.048). Mean fasted live weight (LW) showed a selection line by time interaction (P < 0.001) which reflected greater LW in the early phase of the study in resilient males but increasing for all groups until day 280 before declining and being similar for all groups from day 330. In summary, differences appear to exist in the timing of immune development between these Romney lines, with resistant animals developing immunity earlier and these resistant-line animals also appear to be more physiologically mature at the same chronological age than resilient animals. These observations have implications on the timing of identification and selection of resistant animals.

1. Introduction

Selection of sheep for either resistance or resilience to gastro-intestinal nematode (GIN) parasites are two tools available to reduce the effects of parasites on animal productivity, health and welfare which, when used in combination with other measures, may substantially reduce the reliance on anthelmintics (Bishop et al., 2004). On the other hand, breeding sheep for increased productivity leads to animals that are largely dependent on anthelmintics for acceptable production (Eady et al., 1998; McEwan et al., 1997, 1992; Morris et al., 2010) particularly if there is limited or no concurrent selection pressure for parasite resistance. Animals selected for their enhanced resistance to parasites have been observed to have lesser growth rates (Baker and Gray, 2004; Bisset et al., 2001; Eady et al., 1998; Gamble and Zajac, 1992; Good et al., 2006; Gruner et al., 2003; Matika et al., 2003; Morris et al., 2005; Mugambi et al., 1997) which may reflect priority for nutrients being given to immune functions over growth (Coop and Kyriazikis, 1999;

Coop and Kyriazakis, 2001). Such animals, however, are less attractive to producers particularly in temperate regions where the predominant parasite species have a relatively low level of pathogenicity.

In New Zealand, lines of Romney sheep selected for resistance or resilience to GIN parasites have been established and maintained over several decades resulting in two lines of animals with considerable differences in immunological and parasitological profiles (Bisset et al 1996; Morris et al., 2000, 2010). Resistant-line animals typically have low FEC (Bisset et al., 1991; Morris et al., 1995) whereas resilient-line animals, which have been selected for their ability to maintain production in the absence of anthelmintic, have greater growth rates (Bisset et al., 1996a, 1994; Morris et al., 2010). While it is expected for resistant-line animals to exhibit greater immunological capacity compared with resilient or susceptible animals (Bisset et al., 1996b; Douch et al., 1995, 1994; Green et al., 1999; Shaw et al., 1999, 2012), the difference in timing and the magnitude of immunological responses in these selection lines is less clear and has been suggested to be associated

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with metabolic age, rather than chronological age (Greer and Hamie, 2016). Given that considerable variation exists in the time taken to mature between different breeds and even among individuals of the same breed (Taylor, 1965, 1985), it is possible the development of immunity in resistant line animals may reflect an earlier development of maturity.

Although the acquisition of immunity is known to be costly, studies by Greer et al. (2018) indicated a comparable cost between Romney lines when both lines are given the opportunity to acquire immunity. It is therefore postulated that the difference in performance observed in lines selected for resistance or resilience (de Lautour and de Lautour, 2010; Morris et al., 2000, 1997; Wheeler et al., 2008) may reflect a temporal difference in the timing of immunity and the onset of nutrient partitioning to immune function over growth. Therefore, a better understanding of the timing of immune development in relation to physiological development when exposed to natural infection without anthelmintic intervention may help explain the reported differences in performance in these selection lines. The objective of this study was to test the hypothesis that development of immunity, in part, may be a function of animal maturity through assessing the variations in timing of immunological responses in resistant and resilient Romney selection lines exposed to mixed natural GIN parasite infection.

2. Materials and methods

2.1. Experimental site and animal management

All procedures were carried out with approval from, and in accordance with the Lincoln University Animal Ethics Committee, application number LUAEC #588.

2.2. Animals and sampling

Variation in the timing of development of immunity and immunological responses was assessed in two lines of Romney sheep that had undergone greater than 16 generations of selection either for resistance or resilience to GIN parasites. These lines were established by AgResearch in 1979 (Bisset et al., 1996; Morris et al., 2000) and were actively selected within line initially based on faecal egg count (FEC) and ability to maintain performance without anthelmintic. In 2008 they were transferred to Lincoln University from which point they were maintained without anthelmintic treatment and replacement ewe and ram lambs were randomly selected within each line each year. It must be noted however that criteria existed where animals would be treated if FEC exceeded 1500 epg and weight loss was greater than 10% but these were not reached. Thus, in this context, resistance is defined as the ability to maintain low faecal egg counts and resilience is defined as the ability to maintain performance in the absence of anthelmintic. Twenty-six male and 27 female lambs, which comprised of the total number of the animals born in 2014, were grazed together on paddocks containing predominantly ryegrass pasture to allow for natural infection with mixed parasite species. Of the 53 lambs, 23 were from the resistant (10 rams and 13 ewes) and 30 were resilient (16 rams and 14 ewes) selection lines. From weaning, at a mean 92 days-of-age, animals were sampled approximately every 10 days until 351 days-of-age. No anthelmintic treatment was administered at any time. At each sampling time, faecal samples were collected from the rectum of each lamb immediately upon yarding for the determination of the concentration of nematode eggs in the faeces using a modification of the McMaster method by floatation in saturated sodium chloride solution (M.A.F.F., 1979) where one egg represented 100 eggs per gram (epg). Saliva samples were taken using mouth swabs that were then centrifuged at 1200 x g and the saliva stored at $-20\,°C$ until analysis. Animals were then fasted without access to feed or water for 16 h before the recording of fasted live weights after which they were returned to grazing. Live weights were recorded with the use of electronic identification tags (Allflex New Zealand) and an Aleis tag reader connected to a semi-automated Prattley autodrafter with a precision of 0.2 kg.

2.3. Grazing management

Romney lambs were born and reared on pasture at the Lincoln University Ashley Dene Research Farm and weaned at mean of 92 days-of-age. At a mean of 124 days-of-age lambs were moved to the Lincoln University 'LincolnSheep' Research Farm where they grazed on irrigated pastures and were exposed to continued natural larval challenge comprising mixed-species nematode parasites until 351 days-of-age. Animals had access to *ad libitum* pasture until 280 days-of-age at which point pasture was restricted to a winter grazing allocation. At all times resistant and resilient lambs were grazed together to ensure similar parasite exposure and a similar nutritional environment. From day 215, female and male lambs were separated and grazed separately, and a vasectomised ram fitted with a mating harness was introduced into the female cohorts. The date of the first presence of mating marks on ewe lambs (n = 27) were recorded at subsequent sampling times as an indicator of oestrus to indicate the development of sexual maturity as a proxy for physiological development.

2.4. ELISA analysis

Saliva samples were analysed for antibodies to L3-specific *Trichostrongylus colubriformis* and *Teladorsagia circumcincta* larvae using an enzyme linked immunosorbent assay (ELISA) similar to that described by (Greer et al., 2018). For each of *T. colubriformis* and *T. circumcincta*, 50 μl of somatic L3 antigen/well at 2 μg/ml in coating buffer were incubated at 4 °C overnight in 96-well plates. The ELISA plates were washed 5 times with dilution buffer containing 0.1% (w/v) Tween 20 (W-T20). Then, blocked using 200 μl/well of 10 mM-phosphate buffer at pH 7.2 containing 0.5% Tween-20 and 5% bovine skim milk powder that was incubated for 2 h at room temperature. Plates were then washed 5 times with wash buffer. Diluted saliva (1:10 for IgA and 1:100 for IgG) was added to ELISA plates at 50 μl /well, incubated for 2 h and then plates were washed 5 times with wash buffer. Rabbit anti-sheep IgG (Pierce immunopure Antibodies, cat #31480, lot #GI959969) at a dilution of 1:4000 and IgA conjugated with horse-radish peroxidase Pierce immunopure Antibodies, Lot#A-130 − 108P-35 Bethly Laboratories inc., USA), diluted 1:2000 with ELISA buffer, was added to each well (100 μl) and incubated for 1 h at room temperature. Plates were washed 5 times with wash buffer. To develop colour, 100 μl/well of 0.05 M phosphate-citrate buffer which was adjusted to pH 5.0 with 0.02% of 30% Hydrogen peroxidase (H_2O_2) added and containing 100 μg of tetramethyl benzidine dihydrochloride (Sigma Aldrich, U.S.A) was incubated for 40 min at room temperature. The reaction was stopped by adding 100 μl/well of 1.25 M sulfuric acid (H_2SO_4) and the optical density (OD) at 450 nm read using ELISA plate reader (Multiscan Go, 1510-01462C, Thermofisher Scientific Finland). Results were adjusted according to a standard positive serum sample present on each plate and expressed as the mean optical density (OD) value of duplicate wells.

2.5. Re-classification within selection line

Within each selection line, individual animals were assessed based on observed phenotypic expression on a combination of their capacity to either develop immunity and/or a display of increased growth potential which resulted in four sub-groups, namely: 1) immune and growth (+/+), 2) not immune and growth (-/+), 3) immune with no growth (+/-) and 4) not immune and no growth (-/-). The four traits used were: Live weight (LW), faecal egg count (FEC), immunoglobulin IgG and IgA responses. For immunity, IgG, IgA and FEC were used as indicator traits. For all the traits, a weighted mean;

Weighted mean = [(Mean group1) (N1) + (Mean group2) (N2)] / (N1 + N2)

was used, and an animal needed to have a mean IgG and IgA above the weighted mean whereas for FEC animals needed to have less than the weighted mean, respectively. An animal was deemed as positive for immunity if it had a combination of at least two of the three indicators traits. For classification of positive growth, animals needed to have cumulative live weight gain (LWG) greater than the mean of their respective sex. Animals with similar traits, were then pooled disregarding their initial selection line.

2.6. Statistical analysis

Statistical analysis was performed using Genstat statistical package 18th edition (Version 18.1, VSN International Ltd). Faecal egg counts were log10 (n + 100) transformed prior to analysis with results reported as back-transformed means. Faecal egg counts, IgG and IgA, live weight and relative maturity were subjected to sequential comparison for antedepence structures prior to analysis as repeated measures using a Restricted Maximum Likelihood Model (REML) with time, selection line and sex included as factors and animal as a random factor.

Immunoglobulin G threshold at which animals would be deemed to have developed immunity, was determined by a Receiver Operating Characteristic (ROC) analysis. At any sampling point and for each individual animal, FEC < 200 epg were assigned as true immunity and coded as 1 whereas those ≥200 epg were regarded as false immunity and were coded as 0. These codes were then run paired with the actual corresponding IgG OD-values at each specific sampling time. The resulting correlated values were used to calculate the quality of the test and then plotted with the area under curve giving the probability of having a positive diagnosis test. This analysis suggested an optimum IgG threshold of 1-OD was determined which was associated with FEC < 200 epg, the timing of which animals reached this threshold was then assessed using a one-way ANOVA.

3. Results

3.1. Faecal egg count (FEC)

Mean back-transformed FEC (epg) of female and male Romney from selection lines for resistance or resilience are given in Fig. 1. Overall, FEC showed a selection line by time interaction (P < 0.001) that reflected FEC being similar between lines and initially low and typically remaining at less than 200 epg for resistant-line animals whereas resilient-line animals gradually increased to a peak of 1400 epg at day 230 for females and 1800 epg for males at day 280 before declining to
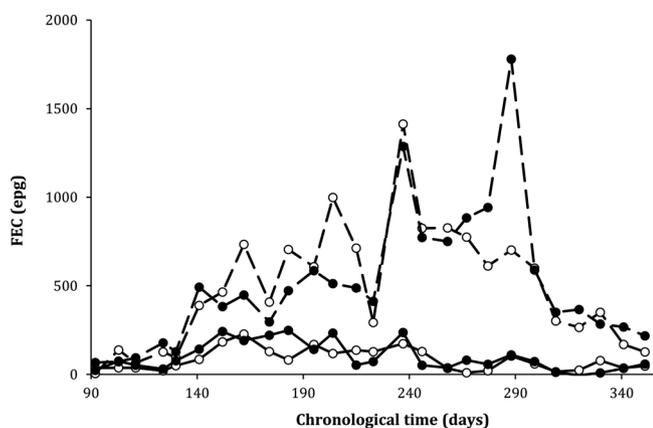
Fig. 1. Mean back-transformed FEC (epg) of resistant (solid line), and resilient (dashed line), males (close circles) and females (open circles) Romney sheep exposed to natural mixed-species GIN parasite infection.
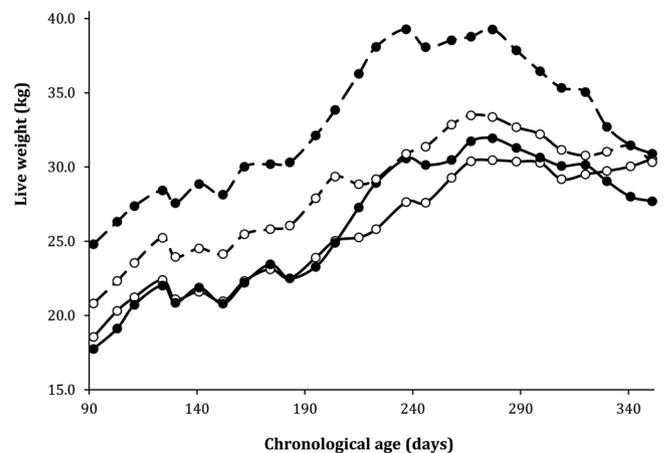
Fig. 2. Mean live weight (kg) of resistant (solid line), and resilient (dashed line), males (close circles) and females (open circles) Romney sheep exposed to a natural mixed-species GIN parasite infection.

less than 500 epg by day 300. There was no effect of sex (P = 0.655) and no interaction between selection line and sex (P = 0.906).

3.2. Live weight (LW) and live weight gain (LWG)

Mean fasted live weight (kg) for female and male resistant and resilient-line animals is given in Fig. 2. At weaning (92 days-of-age), live weight showed a selection line by sex interaction (P = 0.007) reflecting heavier weights in resilient males than their female counterparts whereas male and female resistant animals were similar, viz. 24.9 ± 0.46, 20.8 ± 0.68, 17.7 ± 1.37 and 18.3 ± 0.93 kg for resilient males, resilient females, resistant males and resistant females respectively. Overall, mean fasted live weight showed a selection line by time interaction (P < 0.001) which reflected consistently greater LW in resilient-line animals which peaked at day 280 before declining and being similar for all groups from day 330. Sex had an effect (P = 0.052) reflecting heavier males than females viz. (29.02 ± 0.67 c.f. 27.24 ± 0.73 kg) but there was no interaction between selection line and sex (P = 0.155).

Mean cumulative live weight gain (kg) for female and male resistant and resilient-line animals are given in Fig. 2b. Overall, there were interactions between selection line and time (P < 0.001) and between sex and time (P < 0.001) that reflected live weight gains between days 190 and 260 that were greater for males than females and greater for resilient than resistant animals followed by a greater decline in resilient and in males from day 290.

Cumulative percentage (%) of male and female animals from resistant and resilient Romney selection lines that reached a nominal slaughter weight of 35 kg are given in Fig. 3. Eighty one percent of resilient males reached the slaughter weight by day 215 and 100% by day 277 whereas 20% of resistant male lambs attained this weight by day 215 and 30% by day 277. In female lambs, only 35.7% and 23.1% of resilient and resistant animals reached the slaughter weight by days, 277, respectively.

3.3. Serum immunoglobulin

Mean serum L3 *T. colubriformis* L3-specific IgG and *T. circumcincta* L3-specific IgG profiles are given in Fig. 4a and b, respectively. *Trichostrongylus colubriformis* L 3-specific IgG showed a selection line by time interaction (P < 0.001) reflecting low initial values followed by an increase in all groups with time to similar maximum values at day 330 which occurred earlier in resistant than resilient-line animals. There was no effect of sex on IgG responses (P = 0.159) and no interaction between selection line and sex (P = 0.522) as within selection
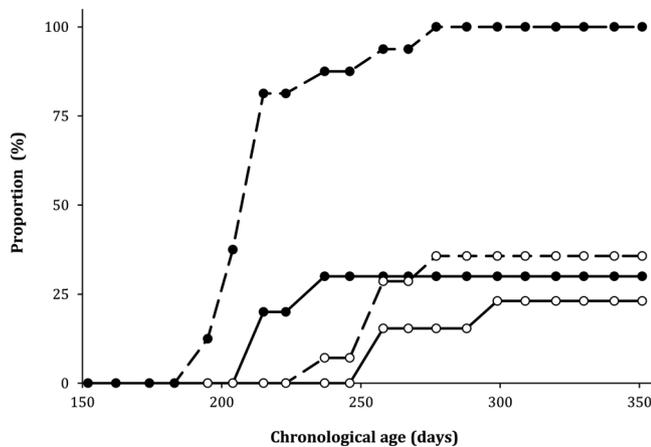
Fig. 3. Cumulative percentage (%) of resistant (solid line), and resilient (dashed line), males (close circles) and females (open circles) Romney sheep that reached a slaughter weight of 35 kg when exposed to a natural mixed-species GIN parasite infection.
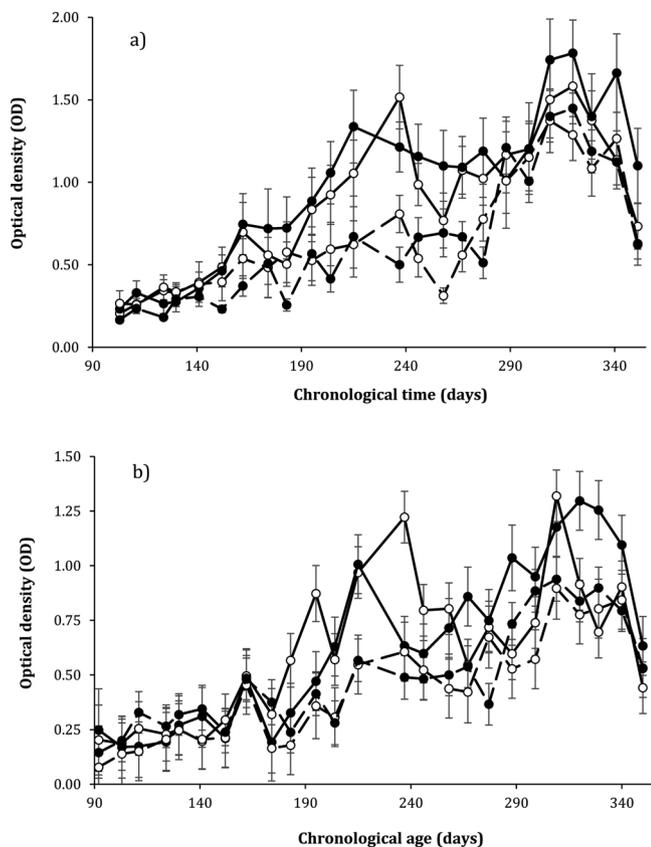

Fig. 4. Mean Optical density (OD) for IgG responses to *T. colubriformis* (a) and *T. circumcincta* (b) L3-specific antigen of resistant (solid line), and resilient (dashed line), males (close circles) and females (open circles) Romney sheep exposed to natural mixed-species GIN parasite infection.

line, both male and females appeared to show similar patterns in their IgG response.

For *T. circumcincta* L3, IgG showed a selection line by time interaction (P = 0.016) reflecting low initial IgG responses which increased with time in all groups up to day 330 but being greater in resistant than resilient counterparts. In addition, the interaction between sex and time was also significant which reflected greater increase with time in resistant females than resistant males between days 215 and 250 and then a subsequent greater response in males than female resistant animals
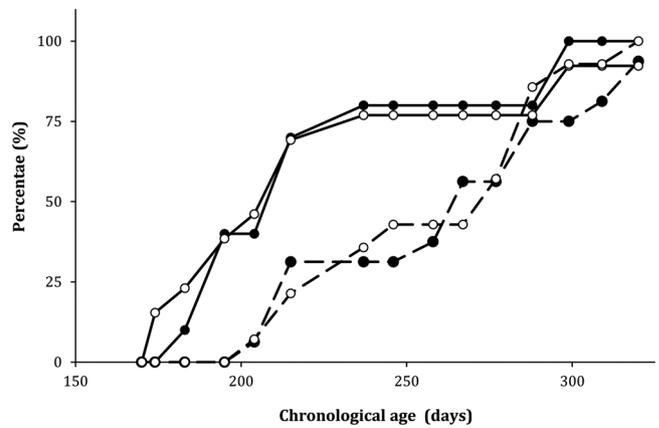

Fig. 5. Cumulative percentage (%) of resistant female (solid line, open circles), resistant male (solid line, closed circles), resilient female (dashed line, open circles) and resilient male lambs (dashed line, closed circles) reaching the threshold IgG response of 1-OD.

between days 320 and 340 whereas IgG for resilient males and females remained similar. However, there was no interaction between selection line and sex (P = 0.684).

3.4. Physiological maturity

3.4.1. Sexual maturity

Overall, the mean age that mating marks were recorded in resistant-ewe lambs was less than their resilient counterparts, viz. 264.2 ± 3.0 days and 274.4 ± 3.4 days, respectively (P = 0.038). Mean live weight at the first record of mating marks tended to be less for resistant than resilient-line females viz. 30.7 ± 1.4 kg c.f. 33.8 ± 0.6 kg respectively (P = 0.066).

3.4.2. Comparison at similar IgG of 1-OD

Cumulative percentages of female and male lambs reaching a threshold IgG of 1-OD is given in Fig. 5. The area under curve (AUC) from the ROC analysis was 0.628 ± 0.020. Overall, mean age of resistant lambs when they reached the threshold IgG of 1-OD was earlier at 220.6 ± 8.8 days-of-age compared with resilient-line animals which reach this threshold at 263.4 ± 6.9 days-of-age (P < 0.001). Within selection line however, the mean age of female and male lambs was similar.

4. Discussion

There were some commonalities but also differences that existed between the selection lines. Both lines showed similarities in the overall response to GIN infection with both reaching a similar magnitude of peak immune markers. Although saliva immunoglobulins as measured here can only serve as a proxy for immune capacity, these results are in contrast with previous reports in animals from these lines which suggested that the magnitude of immune responses are typically greater in resistant compared with resilient lambs (Bisset et al., 1996b; Douch et al., 1995, 1994; Green et al., 1999; Morris et al., 2000; Shaw et al., 1999). It is a commonly held view that resilient-line animals have a lesser immunological capacity when compared with their resistant counterparts, but this did not appear to be the case in the current study although the timing of increase in immune markers and decrease in FEC did differ. Further, both selection lines showed a similar overall pattern in both live weight and live weight gain and they had similar production levels and even FEC by the end of the study. To this end, despite decades of divergence selection for differences in response to GIN parasites, animals from both lines appeared to retain some similar characteristics in their responses to parasite infection.

Some differences did exist between the selection lines, however, they appeared to be temporal. There was a clear and expected difference in the magnitude of the indicator of infection between lines, with mean back-transformed FEC increasing rapidly to reach a peak by day 288 in resilient-line animals whereas FEC for resistant counterparts typically remained low. The corresponding immunological responses, particularly IgG, also remained low in resilient-line animals up until day 260 while for resistant animals, IgG rose only from day 200, despite these animals exhibiting low FEC throughout. These observations are consistent with indoor studies with animals from these selection lines which showed a similar peak but a delayed rise in circulating parasite-specific immunoglobulins in resilient animals (Greer et al., 2018) and provides further support that the difference in between these lines of animals is associated with the timing, rather than magnitude of immune capability. Further, differences in animal performance were observed between these selection lines although much of this was temporal with resilient lambs in the early phase of infection exhibiting a production advantage, which was evident even from weaning. Up until day 280, live weight profiles were consistent with previous reports whereby resilient animals exhibit better growth characteristics than resistant (Bisset et al., 1996a, b; Morris et al., 2000, 1997). In part, this presumably reflects the nutrient partitioning framework as proposed by Coop and Kyriazakis (1999) with resources prioritized to immune development over growth. Direct comparisons of animal performance need to be tempered since, given the necessity to maintain a common nutritional environment and parasitological challenge, all animals were run together. As such, any epidemiological advantage conferred to the resistant animals through reduced nematode egg excretion and which may have influenced their performance was not realized. Nevertheless, the greater performance of resilient lambs during this time despite evidence of a much greater parasite loading indicates a lack of such nutrient prioritization in these animals which presumably reflects a delayed entry onto the nutritionally costly phase of acquisition of immunity (Greer et al., 2009). The impact of this was evidenced by a greater proportion of resilient-line animals and most particularly males being able to reach the arbitrary threshold of 35 kg for slaughter. Although this outcome was likely exacerbated by the restricted winter-feeding regime which reduced the opportunity for continued growth, the delay in obtaining a given slaughter weight ultimately means animals may have to stay longer on-farm, affecting both resource use efficiency and overall farm profitability (Brown, 1990; McIvor and Aspin, 2001; Rendel et al., 2013; Thompson et al., 2016). This was not able to be assessed here as the protocol used in the current study did not factor in either removal of animals once slaughter weight was achieved or the epidemiological advantage of resistance as these were beyond the intended scope of the study. However, both of these aspects seem worthy of investigation in future studies to better mimic farming systems. From day 288 onwards, however, both resistant and resilient lambs had similar live weights which suggests either that resistant lambs were recouping benefits of the earlier nutritional investment of immune development (Greer, 2008) or that greater levels of parasitism were being felt and impacting on resilient animals, an effect which may have been exacerbated by the winter grazing regime which restricted nutrient supply and may have resulted in uncompensated pathological disturbances. Moreover, the greater decline in performance coincided with a rapid increase in immunoglobulin G in resilient lambs and a corresponding reduction in the FEC which suggested more nutrient resources at this time may have been directed towards effecting a strong immune response to counter effects of parasitism at the expense of growth.

At the same chronological age, resistant animals appeared to be more physiologically mature than resilient animals. Although the earlier rise in immunological responses in resistant-line animals and cumulative percentage of animals that reached the threshold IgG of 1-OD may have been anticipated, this occurred at lighter weights relative to their resilient counterparts. Further, resistant-line animals had earlier presence of mating marks, again which occurred at lighter weights

suggesting that they were physiologically more mature at both the same age and lighter live weight. It has been suggested by Greer and Hamie (2016) that immune development to gastro-intestinal nematodes may, in part, be associated with relative maturity. However, it is also clear from the FEC profiles that resistant animals demonstrated a capacity to limit the parasite infection well before a time that can be explained by relative maturity alone and well before there was a clear increase in saliva IgG. Nevertheless, the observation that the rise in immunoglobulin levels and presence of mating marks occurred at a lighter weight in resistant-line animals may help explain some of the differences in performance between these selection lines. In this respect, resistant animals will likely have a lighter mature weight and, given the relationships between mature body weight and growth (Taylor, 1980; Taylor and Fitzhugh, 1971), can be expected to have lower potential growth rates. This has implications for the timing of identification and selection for resistance given the temporal nature of immune development and that selection/ measurement typically occurs at a set chronological age without taking into account physiological age. However, further to this there was evidence of sexual dimorphism in the growth traits between the selection lines whereby resilient males showed greater growth than females but the growth of resistant males and females was similar. The reasons for, and implications of this disparity between the lines are not clear.

Although a majority of animals conformed to expected type, there were some exceptions. Re-classification of individuals that, regardless of original selection line, exhibited either evidence of resistance and/or evidence of resilience is given in Table 1. Although the numbers in each group are low, there were consistent phenotypic markers for re-classified individuals regardless of their original designation. In particular, in both selection lines, animals that grew well had weaning weights > 23 kg while nematode resistance trait alone appears to have favoured animals with lesser growth. These results appear to suggest that opportunity exists to identify animals with both enhanced immune response and growth traits may be possible given a two-stage criteria of weaning weight followed by measurement of either FEC or IgG from 150 days-of-age as given in Table 2. Together, these findings provide support for the suggestion that combined selection for both resistance

Table 1
Proportion of female and male lambs belonging to each of the four subclasses: 1) immune and growth (+/+), 2) not immune and growth (−/+), 3) immune with no growth (+/−) and 4) not immune and no growth (−/−) within resilient and resistant Romney selection lines exposed to mixed-species parasite challenge.

Line of Origin	Sex	Sub-class	No of animals	Percentage (%)
Resilient	Females	+/+	2	**14.3**
		-/+	10	**71.4**
		+/-	1	**7.1**
		-/-	1	**7.1**
		Sub-total	**14**	
	Males	+/+	3	**18.8**
		-/+	12	**75.0**
		+/-	0	**0.0**
		-/-	1	**6.3**
		Sub-total	**16**	
		Total	**30**	
Resistant	Females	+/+	4	**30.8**
		-/+	1	**7.7**
		+/-	6	**46.2**
		-/-	2	**15.4**
		Sub-total	**13**	
	Males	+/+	3	**30.0**
		-/+	0	**0.0**
		+/-	6	**60.0**
		-/-	1	**10.0**
		Sub-total	**10**	
		Total	**23**	
		Grand Total	**53**	

Table 2

Characteristics of weaning weights (kg), immunoglobulin G at 220 days and sampling for FEC at 270 day-of-age in Romney sheep lambs grouped in four subclasses: 1) immune and growth (+/+), 2) not immune and growth (−/+), 3) immune with no growth (+/−) and 4) not immune and no growth (−/−).

Weaning weights	Sex	Subclass	# of animals	# of animals with FEC > 500 at day 277	Percentage (%) within sex group	Mean LWG (kg) at day 277	Mean FEC (epg) at day 277	Mean LWG (kg) at day 351	Mean FEC (epg) at day 351	Mean age at 1-OD IgG
> 23 kg	Female	+/+	4	1	25	12.2 ± 1.2	200 ± 168	6.7 ± 0.6	221 ± 65	241
		+/−	0	0	N/A	N/A	N/A	N/A	N/A	N/A
		−/+	3	2	67	11.1 ± 2.2	1300 ± 874	5.5 ± 1.3	570 ± 265	288
		−/−	0	0	N/A	N/A	N/A	N/A	N/A	N/A
		Sub-total	**7**							
	Male	+/+	6	2	33	16.7 ± 0.9	300 ± 179	9.7 ± 0.9	265 ± 55	214
		+/−	0	0	N/A	N/A	N/A	N/A	N/A	N/A
		−/+	12	10	83.3	14.4 ± 0.5	2483.3 ± 598.7	8.4 ± 1.0	957.2 ± 131.7	288
		−/−	1	1	100	12	3700	5.4	968	288
		Sub-total	**19**							

Weaning weights	Sex	Subclass	# of animals	# of animals with FEC > 500 at day 277	Percentage (%) within sex group	Mean LWG (kg) at day 277	Mean FEC (epg) at day 277	Mean LWG (kg) at day 351	Mean FEC (epg) at day 351	Mean age at 1-OD IgG
< 23 kg	Female	+/+	2	0	0	13.4	50	9.4	145.6 ± 13.6	215
		+/−	7	0	0	11.1 ± 0.6	42.9 ± 20.2	6.7 ± 0.4	149.1 ± 44.7	199
		−/+	8	4	50	14.2 ± 1.2	1087.5 ± 454	9.1 ± 0.5	682.9 ± 156.0	266
		−/−	3	1	33.3	12.8 ± 0.3	300 ± 208.2	8.1 ± 1.0	252.5 ± 146.9	278
		Sub-total	**20**							
	Male	+/+	0	0	N/A	N/A	N/A	N/A	N/A	N/A
		+/−	6	0	0	13.1 ± 0.9	50.0 ± 34.2	7.9 ± 0.6	118.0 ± 24.7	222
		−/+	0	0	N/A	N/A	N/A	N/A	N/A	N/A
		−/−	1	0	0	13.4	100	8.4	171	288
		Sub-total	**7**							

and resilience is possible (Bishop and Morris, 2007; Bisset and Morris, 1996) but the resulting genetic relationship may depend on the balance between the two seemingly opposing traits (Bishop, 2012; Bishop and Stear, 2003) as both traits (immunity and growth) compete for nutrient resources (Sykes et al., 1979; Coop and Kyriazakis, 2001). Clearly this is limited by the population size and the environment and species of parasite challenge in this environment, but the consistency of the resistant + resilient phenotype in animals disregarding their original selection line, which may be considered to represent extremes of the expected response to infection, seems worthy of consideration.

Conflicts of interest statement

The authors declare no conflicts of interests.

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