Genetics of Resistance to *Haemonchus contortus* infections in sheep

by

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(ABSTRACT)

Genetic control of resistance to *H. contortus* was assessed in 198 ewes and 386 lambs of 50% Dorset, 25% Rambouillet and 25% Finnsheep breeding in fall and spring over 2 yr. After deworming, lambs that were approximately 120 d old and ewes that had weaned their lambs at 60 d and dried off were individually dosed with approximately 10,000 infective larvae. After infection, body weight (BW), fecal egg counts (FEC) and packed cell volume (PCV) were measured weekly for 7 wk in lambs and fortnightly for eleven wk in ewes. Summary traits were defined as initial PCV, mean BW (MBW) across all times, and means for FEC, log-transformed FEC (MLFEC), and PCV (MPCV) at wk 3 to 7 post-infection for lambs and wk 3 to 11 post-infection for ewes.

No consistent seasonal variation in FEC was observed. Younger ewes were more susceptible to infection than older ewes. Sex differences in FEC were not observed in lambs.

Heritabilities for summary traits were estimated from a REML analysis that included fixed effects of year and season plus effects of either sex (for lambs) or age category (for ewes). Heritability estimates for MBW, MPCV, and MLFEC were 0.74, 0.57, and 0.27 respectively (all $P < 0.01$), in lambs, and 0.24 ($P < 0.1$), 0.25 ($P < 0.05$) and 0.55 ($P < 0.01$), respectively, in ewes. Across-year repeatability estimates in ewes for MBW, MPCV, and MLFEC were 0.83, 0.54 and 0.56, respectively (all $P < 0.01$). Resistance was antagonistically associated with estimated breeding values for growth in ewes but not in lambs. Fertility and prolificacy in ewes were not related to resistance.

Breed differences in resistance to *H. contortus* were also evaluated in 4 to 6-mo-old crossbred Dorset and Dorper, straightbred Katahdin, and Barbados Blackbelly x St. Croix lambs. Dorpers were not more resistant than Dorsets but appeared to cope better, with higher PCV and similar BW during infection compared to Dorsets. Katahdin and Barbados Blackbelly x St. Croix lambs were more resistant with lower FEC.

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INTRODUCTION

Gastro-intestinal nematode parasite infections are a major constraint to the sheep industry and cause production losses, increased costs of management and treatment, and even mortality in severe cases (Barger and Cox, 1984; Larsen et al., 1995). There have been several reports of endoparasites becoming resistant to most of the available classes of anthelmintics (van Wyk and Malan, 1988; Overend et al., 1994). In light of the emerging anthelmintic resistance and consumer demands for animal products that are produced without the use of chemical products (organically produced), research in the past two decades has been focused on other viable methods for controlling helminthiasis in sheep.

Over the past several years, evidence has emerged that suggests a genetic basis for resistance to gastro-intestinal nematodes in sheep. Differences exist both between and within breeds in response to infection. Some breeds of sheep, such as St. Croix and Red Maasai, are more resistant to nematode infections than other breeds (Courtney et al., 1985a, 1985b; Gamble and Zajac, 1992; Wanyangu et al., 1997); shifting to resistant breeds, or designing cross-breeding programs involving resistant sheep breeds, are thus viable options in combating nematode infections. Resistance to *Haemonchus contortus* has been also shown to be moderately heritable (Woolaston and Piper, 1996; Albers et al., 1987), indicating that selection and breeding of sheep for increased resistance is possible. 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 the United Kingdom (Bishop et al., 1996; Bishop and Stear, 2001); there has been limited research in the United States in recent years. Genetic parameter estimates for resistance traits are not available for *Haemonchus* infections in the US although infections exist and are widespread.

The objectives of this thesis were to describe the response of sheep to infection with *H. contortus*, to obtain genetic parameter estimates for resistance to infection in ewes and lambs, to evaluate the relationships between parasite resistance traits and production traits, and to assess breed differences in response to infection with *H. contortus*.

CHAPTER 1

LITERATURE REVIEW

Life cycle of *Haemonchus contortus*

H. contortus is a blood sucking gastro-intestinal nematode parasite belonging to the family Trichostrongylidae. The typical life cycle begins when the adult female lays eggs that are passed out in the feces of the animal. Hatching of the eggs is controlled by temperature and humidity and also to an extent by the larva within the egg. Once the first-stage (L1) larva hatches, it molts to form the second-stage (L2) larva. These two stages are free-living pre-parasitic forms that feed on the bacteria in the fecal material. The L2 larva molts to form the third-stage (L3) larva but retains the cuticle of the second stage larva; as a result, it cannot feed and has to rely on stored nutrients for energy and metabolism. Development from L1 to L3 takes about 5 d under optimal conditions (18 to 26°C and 80 to 100% humidity), but under cooler conditions can take several weeks or months. The optimal temperature for survival of L3 is about 18 to 26 °C. At lower temperatures, L3 can survive for several months as the metabolism slows down and the energy supplies last longer. Humidity is also an important factor in survival of the larva; dry conditions are not favorable for larval survival. Infection is by ingestion of L3 and is followed by its exsheathment. Two moltings later, the L5 or immature adult is formed which develops a lancet, pierces the mucosal vessels, and starts sucking blood. The site of prediliction is the abomasum (Bowman, 1995).

An important phenomenon observed in the life cycle that has epidemiological implications is "arrested larval development" or "hypobiosis". Hypobiosis is the "temporary cessation of development of a nematode at a particular point in its parasitic development" (Urquhart, 1996). It is usually due to an unfavourable environmental stimulus, such as cold weather or dry conditions, received by the free-living L3 prior to ingestion and usually coincides with onset of winter or very dry conditions. Arrested development can occur in the gut of sheep or on pasture and ensures survival of the nematode under adverse climatic conditions. Subsequent maturation of the larvae due to resumption of development known as the 'spring rise', when favorable conditions return in the spring, leads to a rapid rise in infection levels or fecal egg counts in the sheep.

Symptoms, treatment and control, and effect on production of *Haemonchus* infections

In cases of severe *Haemonchus* infection, the most obvious symptoms are progressive weight loss and anaemia. Packed cell volumes (PCV) drop about 10 to 12 d post-infection. Animals may become anemic during the course of infection if left untreated, with pale gums and insides of eyelids and can even die. Serum iron and albumin levels may decline about 10 d post-infection and this results in "bottle-jaw" (due to hypo-proteinemia) condition due to edema of the lower jaw and neck region (Altaif and Dargie, 1978b). In the case of chronic infection with *Haemonchus*, the signs are not very obvious although there is a mild drop in the packed cell volumes and lower weight gains compared to uninfected sheep (Barger and Cox, 1984). In the case of hyperacute hemonchosis, sheep may die suddenly as a result of hemorrhagic anemia caused by severe blood loss from the gut.

Diarrhea is not a common symptom of haemonchosis as the intestines are not usually affected, in contrast to other endo-parasitic infections such as *Trichostrongylus* infections. Diarrhea leads to accumulation of fecal material on the hindquarters of sheep, also called "dags", which lowers the value of the fleece and may lead to losses of up to $10 million in high rainfall regions in Australia (Larsen et al., 1995).

Production is adversely affected by the presence of nematode parasites. Live weight gains are lower, and there may be weight loss and even mortality in severe infections, especially if the diet is deficient in protein. Live weight gains and greasy fleece weights are higher in breeding ewes treated with anthelminthics than in those left untreated (Larsen et al., 1995), although Barger and Cox (1984) did not find wool production of chronically infected sheep to be lower than in uninfected sheep. Economic losses are primarily due to mortality, although losses in production can also be high (Barger and Cox, 1984).

Trichostrongyle infections can be diagnosed by examination of the feces for parasite eggs (McKenna, 1981). Eggs can be found in the feces about 2 to 3 wk post-infection, and fecal culturing can be done to identify the genus of larvae. Fecal egg counts (FEC) are representative of the worm burdens carried in the gut of sheep and goats (Cabaret, 1998). Treatment involves use of anthelminthic drugs such as benzimidazoles, levamisole and ivermectin, among others. However, these drugs are becoming ineffective against many trichostrongylid parasites that affect sheep in several parts of the world (Miller and Barras 1994; Waruiru et al., 1998; Gopal et al., 1999). Present research indicates that the disease can be controlled to an extent by providing better nutrition (especially protein supplementation to lambs), rotational grazing, strategic drenching at times of heightened risk of infection, pasture management (Barger, 1999), and perhaps biological control using fungi (Larsen et al., 2000). Vaccination for improved immunity to *H. contortus* also appears to be promising (Smith, 1999), but is not yet practical.

Immune response of host against infection

Sheep respond to infection by trichostrongylid parasites by mounting an immune response that affects the parasite in several ways. However, this immune response is reported to be acquired rather than innate (Bishop et al., 1996; reviewed by Stear and Wakelin, 1998; Stear et al., 1999; Gamble and Zajac, 1992). This means that, in most cases, a primary infection will lead to higher FEC or lower PCVs compared to secondary infections. Response to primary challenge can be influenced by age, with older animals showing a better response (Gamble and Zajac, 1992).

At the cellular level, *Haemonchus* produces a response that is characterized by increased numbers of globule leucocytes (mucosal mast cells that have released their granules), mucosal mast cells, and eosinophils in the abomasal mucosa (Bradley et al., 1973; Gill, 1991; Zajac et al, 1990). Resistant sheep have higher numbers of these cells when compared to susceptible sheep (Bradley et al., 1973; Bisset et al., 1996; Salman and Duncan, 1984; Gamble and Zajac, 1992). The eosinophils and globule leucocytes are responsible for expulsion of the worms from the gut and thus prevent establishment of the parasite (Bradley et al, 1973; Rainbird et al., 1998; Balic et al., 2002). Sensitization of the mucosal mast cells during primary infection has been reported to

be associated with development of acquired resistance to *Haemonchus* infections (Bendixsen et al., 1995).

Humoral response is seen in terms of increased levels of parasite-specific immunoglobulins including IgA (Gill et al., 1994; Strain and Stear, 2001), and IgG and IgM (Bisset et al., 1996). IgA appears to affect worm growth and fecundity (Strain and Stear, 2001). Lambs appear to achieve resistance by controlling worm growth and fecundity rather than worm numbers, whereas older sheep can control both, and therefore have much lower FEC than lambs (Stear et al., 1999). Overall, genetic resistance to gastro-intestinal nematodes is acquired and reflects both cell-mediated and humoral immune responses.

Factors affecting resistance to infection

There are two broad concepts relating to the ability of the animal to withstand infection – one of resistance and the other of resilience. Resistance is defined as the ability of the host to resist establishment of the parasite and refers to ability of the host to modify the growth and fecundity of the parasite. On the other hand, resilience is defined as the ability of the host to thrive in the presence of the parasite and reflects the response of the host to infection by the parasite (Gray, 1995; Gray and Gill, 1993).

There are several factors that affect the ability of the host to resist or cope with infection. Some of the important documented factors are age, sex, nutrition, reproductive status, breed (between-breed variation) and the animal itself (within-breed variation).

Age. Lambs appear to be less resistant to infection than adult sheep. Courtney et al. (1985a) found that age did not seem to have a major effect on resistance in case of sub-tropical breeds such as St. Croix, Florida Native and Barbados Blackbelly, but that domestic crossbred lambs of Dorset, Suffolk, and Finnsheep ancestry seemed to become more resistant after puberty at about 8 to 9 mo of age, with higher FEC in younger lambs.

Gamble and Zajac (1992) found that age affected resistance to a primary infection in both St. Croix and Dorset breeds as reflected by lower egg production in older lambs (15 wk of age) compared to younger lambs (8 wk of age). Kambara et al. (1993) found that Dorset crossbred sheep vaccinated at 8 to 20 wk of age were more susceptible to infection with *T. colubriformis* than older sheep vaccinated at 33 wk of age when both were raised on a low protein diet. The authors suggested that this might be due to the increased lymphocyte responsiveness to L3 antigen in older vaccinated lambs.

Younger lambs appear to not be capable of mounting a strong acquired immune response against the parasite and thus are less resistant. Acquired resistance improves with age. Ewes therefore generally have lower FEC than lambs, although peri-parturient ewes may experience rather heavy infections.

Sex. Male sheep appear to be more susceptible to parasitic infections when compared to female sheep. Courtney et al. (1985a) found females were more resistant to infection and had lower FEC than males after puberty, although there were no differences before puberty. Barger

(1993) reviewed the effect of host sex on resistance levels. He reported several studies that indicated that male sheep were more susceptible than females in natural and experimental infection with *T. colubriformis* and *H. contortus*. These differences were observed around or after puberty, and no differences were observed prior to puberty. He also reported that these differences may be due to a stimulatory effect of estrogens on immune responses and that androgens may actually have an opposite effect.

Nutrition. Nutrition and especially protein supplementation, has a favorable effect on resistance to parasitic infections. Preston and Allonby (1978) found that 2- to 3-yr old sheep receiving a higher protein diet (3.5 g CP/kg bwt/d) were more resistant to infection than animals maintained on a low-protein diet (1.7 g CP/kg bwt/d). Also, animals on a higher protein diet showed a self-cure reaction 13 wk post-infection whereas those on a low-protein diet did not show such a reaction, suggesting an immunological self-cure was more likely to occur in well-fed animals. Kambara et al. (1993) found that resistance was lower in vaccinated sheep receiving a low-protein diet (11% CP) compared to vaccinated sheep receiving a high-protein diet in sheep aged 8 to 20 wk. Dutta et al. (1999) also reported that sheep fed a higher protein diet for a short period of time during the post-weaning period had lower FEC under natural pasture conditions than those fed a lower protein diet even when protein supplementation was no longer provided.

Reproductive status. Ewes become more susceptible to infection and thus show a peri-parturient rise (PPR) in the FEC around the time of parturition, beginning around 2 wk prior to lambing and continuing up to weaning of the lambs (Courtney et al., 1984; Baker et al., 1999). The PPR may be due to a temporary relaxation in immunity, possibly but not certainly associated with increased serum prolactin levels (reviewed by Barger, 1993). The PPR causes increased pasture contamination at the time of lambing and greatly increases the chances of infection in the very susceptible young lambs. Resistant breeds like St. Croix and Florida Native may or may not show PPR but they certainly have a lower PPR than temperate breeds like Rambouillet or Dorset x Rambouillet (Courtney et al., 1984; Zajac et al., 1988). Selection of Florida Native ewes for reduction in FEC by grazing them on contaminated pastures without anthelminthic treatment also led to a reduction in PPR (Courtney et al., 1986). Woolaston (1992) reported that lambs selected for increased or decreased resistance to *H. contortus* exhibited similar differences in resistance as peri-parturient ewes. However, Courtney et al. (1986) suggested that selection for reduced PPR in ewes might not improve resistance in the progeny because the correlation between FEC of dams and their ewe lambs was not significant. They suggested that acquired resistance in young lambs and PPR in ewes are controlled by different genetic mechanisms. The PPR is also affected by reproductive performance of the ewe; ewes with twins show a higher PPR than ewes with singles (Courtney et al., 1986; Bishop and Stear, 2001).

Between breed variation. Some breeds are more resistant to infection than others. In a study conducted by Bradley et al. (1973), Florida Native lambs, raised worm free and given two doses of infective *Haemonchus* larvae at 5.5 to 6 mo of age, had higher weight gains and mean PCV during infection than did Rambouillet lambs given one dose of infective larvae. Florida Native lambs showed greater eosinophilic infiltration in the abomasum 2 wk post-infection; no infiltration was observed in Rambouillet lambs. Florida Native lambs had smaller worm burdens (the number of worms counted in the gut) than Rambouillet lambs, which was attributed to

greater eosinophilic infiltration in the abomasal mucosa with associated expulsion of worms. The authors concluded that inhibition of larval stages, prolonged pre-patent period, increased eosinophilic infiltration of abomasal mucosa, and a more rapid self-cure reaction enable the Florida Native to resist infection, and that these reactions were manifested by the lower adult worm populations, higher PCV and greater body weight gains.

Altaif and Dargie (1978a) compared the response to primary infection with *H. contortus* in 7- to 10-mo old Finn-Dorset and Scottish Blackface lambs raised parasite free from birth. Scottish Blackface lambs had higher PCV and lower FEC and worm burdens than Finn-Dorset lambs. They also experienced less blood loss from the gut compared to the Finn-Dorset. Scottish Blackfaces were also more resistant to re-infection with *H. contortus* (Altaif and Dargie, 1978b).

Todd et al. (1978) did not find any breed differences in response to *H. contortus* infection between Barbados Blackbelly x Targhee and straightbred Targhee in lambs that were raised worm-free and then infected with different doses (10,000 and 25,000) of larvae at 4 mo of age, although lambs receiving a heavier dose had much higher FEC and worm burdens, and lower PCV post-infection. However, Barbados Blackbelly x Dorset lambs had lower FEC than Dorset lambs in response to a mixed challenge, both on pasture or with artificial oral infection (Yazwinski et al., 1979), and also in response to an artificial *H. contortus* challenge (Yazwinski et al., 1981).

Courtney et al. (1985a) reported in lambs of 4 to 6 mo of age, experiencing a secondary infection with *H. contortus*, that St. Croix lambs were more resistant than domestic crossbred lambs (½ - Suffolk, ¼ - Dorset, ¼ - Finnsheep or ½ - Dorset, ¼- Finnsheep, and ¼- Rambouillet). Florida Native, Barbados Blackbelly and ¾ - St. Croix lambs were intermediate. Variations among breeds were not consistent in response to primary infection. This result suggests that observed breed differences may be due to differences in acquired immunity. Similar results were obtained in 9-mo-old lambs around the time of puberty. St. Croix were more resistant than domestic crossbred lambs.

Zajac et al. (1990) found that 9- to 10-month-old Dorset x Rambouillet lambs were less resistant to infection with *H. contortus* than age matched St. Croix and Florida Native lambs. However, contrary to the findings of Courtney et al. (1985) and Bradley et al. (1973), there were no breed differences in worm burdens, indicating that breed differences in FEC may have been due to differences in immune response affecting parasite fecundity. However, the authors also suggested that the observed results might have been due to individual variation in parasite challenge superseding breed differences in the small experimental group (n=48 total) or that sheep were slaughtered too soon (2 wk after infection) for breed differences in worm burdens to have been observed.

In a study that compared resistance of St. Croix lambs to that of Dorset lambs under experimental and natural infections with *H. contortus*, Gamble and Zajac (1992) found no significant differences between the breeds in FEC in response to primary experimental infection at 8 wk of age, but when challenged again after deworming at 14 wk of age, the St. Croix had fewer eggs compared to the Dorsets. The egg counts observed in response to the primary

infection were greater than those observed in response to the later infection. In conditions of natural infection, significant breed differences were noticed beginning 47 d after first exposure at 8 wk of age, and then again at 24 d after drug treatment and re-infection. St. Croix lambs had fewer eggs compared to Dorsets. St. Croix lambs had more than 99% fewer worms in the abomasum compared to Dorset lambs and had 15 to 40 times more globule leucocytes in the abomasal mucosa than Dorsets. St. Croix lambs appeared to be more refractory to re-infection and had higher levels of acquired resistance in response to both natural and experimental infections with *H. contortus*.

In Africa, the Red Maasai breed has been reported to be relatively resistant to *Haemonchus* infections. Preston and Allonby (1978) compared resistance after an artificial *Haemonchus* infection in Red Maasai, Corriedale, Merino, and Hampshire Down sheep at 2 to 3 yr of age. Red Maasai had consistently lower FEC during the 14-wk post-infection observation period. Hampshire Down had the highest FEC, while Merino and Corriedale were intermediate. Similar results were observed for worm counts made 4 wk post-infection. More recently, 10 to 15 mo old Red Maasai wethers have been shown to be more resistant to natural and artificial *Haemonchus* infections, with lower FEC and higher PCV compared to Dorpers, Blackheaded Somali, and Romney-Marsh sheep (Mugambi et al., 1997). Wanyangu et al. (1997) found similar results when comparing Red Maasai and Dorper ewes facing either an artificial or a natural pasture challenge with *Haemonchus*. Red Maasai ewes also exhibited a significantly lower PPR in FEC than Dorper ewes. Baker et al. (1999) compared Red Maasai, Dorper, and Red Maasai x Dorper ewes for resistance to a natural (predominantly *Haemonchus*) pasture infection. They measured FEC and PCV at mating, 3 mo after mating, 1 wk before lambing and 1, 2, and 3 mo post-lambing over a period of 4 yr. Red Maasai ewes to had a lower FEC and higher PCV than Dorper ewes at most sampling times. Red Maasai x Dorper ewes were as susceptible as the Dorpers at most sampling times.

Comparisons between non-lambing ewes of sub-tropical and temperate breeds facing a natural parasite challenge in fall did not reveal any breed differences in resistance (Courtney et al., 1985b). However, the numbers of animals involved in the study were too few to make a decisive conclusion. In an earlier study, Courtney et al. (1984) found that Florida Native, Barbados Blackbelly and St. Croix ewes showed no PPR in FEC when housed from late fall through lambing and weaning, whereas Rambouillet and Finn-Dorset x Rambouillet showed pronounced PPR 6 to 7 wk after lambing under similar conditions and had higher FEC than the sub-tropical breeds. Crosses of St. Croix and the domestic ewes (represented by Rambouillet and the Finn-Dorset x Rambouillet) showed an intermediate PPR. When the ewes were allowed to graze on pasture, all showed PPR by about 8 wk after lambing but Florida Native, three-quarter St. Croix and St. Croix ewes had lower FEC than domestic ewes.

Within-Breed Variation. Some of the earliest reports of within-breed variation in response to helminth infections were made in the United States of America (Stewart et al., 1937; Gregory et al., 1940; Whitlock, 1955; Scrivner, 1967) with focus shifting to Australia and New Zealand in the more recent years.

Most research in Australia has focused on two of the most important gastro-intestinal nematode parasites, namely *H. contortus* and *T. colubriformis*. Lines of Merino sheep have been established with diverging responses to both these parasites.

Windon et al. (1980) sought to study the response of young random-bred Merino lambs to vaccination with irradiated *T. colubriformis* larvae in order to classify them into "responders" and "non-responders". Responders were lambs that had FEC below the lower 90% confidence limit of unvaccinated control lambs. Lambs that had been raised worm-free received one, two or three vaccinations at 1, 2 and/or 3 mo of age. Simultaneously, an extended primary challenge with *T. colubriformis* larvae was also given. Secondary challenge was given at about 6 mo of age with a single dose of 10,000-*T. colubriformis* larvae. Lambs differed in their response to vaccination in terms of their FEC following primary challenge and were classified as responders or non-responders; these also differed in their response to secondary challenge. Responses of lambs to primary and secondary challenge were highly correlated. The authors concluded that there was a significant genetic component involved in the responsiveness of young lambs to vaccination.

Dineen and Windon (1980) used ten 18-mo-old rams selected based on results of the previous experiment (Windon et al., 1980) and mated them to unselected ewes to determine if breeding for increased resistance to internal parasites was feasible in Merinos under field conditions. Five of the rams were top-ranked "responders" and the other five were the lowest ranked "non-responders". The lambs were vaccinated at 8 and 12 wk of age with 20,000 irradiated *T. colubriformis* larvae, dewormed at 16 wk of age and challenged with 20,000 infective larvae 1 wk later. Both wether and ewe progeny of responder sires had lower FEC compared to progeny of non-responder sires. Also, vaccination was most effective in responder progeny of the responder sires and responder sires had very few non-responder progeny. Performance of the ewe and wether half sibs was highly correlated, indicating a strong influence of sire genetics on the performance of the progeny. The authors concluded that sire selection would lead to substantial progress in improvement of responsiveness of lambs to vaccination against *T. colubriformis.*

When Windon and Dineen (1981) assortatively mated the ten sires to groups of ewes classified as responders and non-responders as lambs by Windon et al. (1980), better progress was seen in the F_1 progeny in responsiveness to vaccination when compared to sire selection alone (Dineen and Windon, 1980). Such assortative matings were carried out for several generations to establish "high response" and "low response" lines.

Woolaston and Windon (2001) reported genetic parameter estimates from these lines of sheep. They used animals from the start of the establishment of the line in 1975 until the 1996 lamb crop. The testing protocol until 1988 was as described before (Dineen and Windon, 1980). From the next lamb crop (born in 1991) on, lambs were tested on pasture. After weaning at 14 wk of age, lambs were dewormed at 16 weeks of age and infected at 17 wk of age with 20,000 infective larvae. FEC measurements were taken at 3, 4 and 5 wk post-infection, after which all animals were dewormed. They were dosed again at 23 wk of age and similar measurements were taken. Heritability estimates for the average FEC for the pen-tested animals was 0.39±0.05, that for primary challenge in field-tested animals was 0.21±0.06 and that for secondary infection

in field-tested animals was 0.37±0.07. Heritability for individual measurements varied from 0.33 to 0.39 for animals challenged in the pen, and from 0.27 to 0.33 in secondary infections of the field-tested animals. Genetic correlations between adjacent individual FECs within all infections were 0.9 or larger; correlations among all measurements in the pen-tested animals were generally 0.78 to 0.81. Genetic correlation between average pen- and field-tested FEC was 0.7 and that between the two field-tested FEC averages was 0.9. The authors concluded that in case of pen-tested animals, a single measurement would have been sufficient because averaging all the measures did not greatly increase heritability compared to individual measurements and because of the high genetic correlations between individual measures. They also concluded that testing in pens would not increase heritability appreciably when compared to testing under field conditions following an artificial infection. Also, one measurement taken 3 to 5 wk post-infection in previously sensitized lambs would lead to maximum genetic progress in reducing FEC in pasture-reared animals.

Albers et al. (1987) studied the genetics of resistance and resilience in 4- to 5-mo-old fine-wool Merino lambs artificially infected with *H. contortus*. They also estimated the genetic relationships among resistance, resilience and production characteristics. Heritability estimates for FEC and PCV, the resistance traits, were about 0.3±0.1 and 0.4±0.1 respectively. Live weight gain depression, wool growth depression and fleece diameter difference, which measured differences in production between infected and uninfected animals, were used as indicator traits of resilience. None had heritability estimates that were significantly different from zero. Fecal egg counts and PCV had a strong negative correlation. There was no significant correlation between resistance and productivity in uninfected animals, indicating that selection for resistance will not have an unfavorable effect on production potential. Resistance traits (FEC and PCV) had a favourable genetic correlation with wool growth but an unfavourable relationship with fiber diameter during infection. In general, resistant animals were found to have reduced FEC, increased PCV, increased weight gain and wool production, and also increased fiber diameter. However, Eady et al. (1998) found a positive (unfavorable) genetic correlation between fleece weight and FEC. Albers et al. (1987) found a significant sire-group effect on resistance. One particular sire group was remarkably resistant, with consistently low fecal egg counts, higher PCV, and average growth rate. The sire involved was named the "Golden Ram" and this discovery led to the reasoning that inheritance of resistance might be due to one or several closely linked loci. Whitlock et al. (1955) had also reported an extremely resistant sire named Violet. The authors concluded that selection for resistance would bring more progress as it was more heritable than resilience and given the moderately positive genetic correlation between resistance and resilience, production of infected animals would also improve. The authors suggested use of production measures in infected animals and resistance to infection as selection criteria to maximize benefits in a breeding program.

Woolaston et al. (1990) studied the response to helminth infection in lines of sheep selected for increased and decreased resistance to *H. contortus* for approximately four generations. Selection was based on FEC following an artificial *H. contortus* infection at 4 to 6 mo of age. Fecal eggs counts were lower and PCV were higher in the increased resistance line when compared to the random-bred control line and the decreased resistance line. Generally, when compared to the control line, the increased resistance line had 79% lower FEC and the decreased resistance line had 37% higher FEC. Differences of such a magnitude should reduce

the requirement for anthelmintic treatment significantly (Barger, 1989). Furthermore, the difference persisted under natural infections (predominantly *H. contortus*) and a later artificial infection with *T. colubriformis* at 7 to 9 mo of age. These results suggest that resistance to infection with one parasite species also confers some degree of resistance to other parasite species and to a natural field challenge. The difference between these lines also persisted when the selected lambs were tested as ewes during the peri-parturient period (Woolaston, 1992). This result suggests that testing for resistance as lambs will be useful not only in improving resistance in lambs but also in reducing the numbers of infective larvae deposited on pastures by lactating ewes.

Heritability estimates similar to those reported by the Australians have been reported from New Zealand conditions (Watson et al., 1986; Bisset et al., 1992). However, in contrast to most Australian studies, New Zealand researchers have used natural field challenges to test sheep for resistance to internal parasite infections.

Bisset et al. (1992) used an extended period of natural infection, consisting mostly of *T. colubriformis* and to an extent some *Ostertagia spp*. and *Cooperia spp*., to estimate heritability of FEC in a commercial flock of Romney sheep. Lambs were drenched soon after weaning at about 3 mo of age and then remained undrenched until 7 to 8 mo of age. Dag scores (which measure the degree of soiling of the breech region due to diarrhoea) and fecal egg counts were measured in all lambs after average FEC in a monitor group reached 1,000-1,500 eggs per gram. Heritabilities of FEC and dag score were 0.27 and 0.24, respectively. Animals with higher FEC also had lower weight gains and higher dag scores. Fleece weight and FEC had a negative genetic correlation of -0.31±0.16. This correlation was in the same direction as the Australian finding, although somewhat smaller in magnitude. The authors concluded that using an independent culling levels approach involving FEC, dag score, and growth rates when infected might be the best approach to improve resistance to internal parasites.

At the Wallaceville Animal Research center, selection lines of Romneys were established in 1979 based on consistently high or low FEC following successive periods of mixed natural challenge between 3 and 8 mo of age. Heritability for individual FEC measures ranged from 0.29 to 0.42; the third FEC measure, taken at 7 to 8 mo of age, was most heritable (Morris et al., 1997). By 1992, the two lines differed in their FEC by 2.9 genetic standard deviations. These lambs also differed in their peri-parturient FECs as ewes (Morris et al., 1998); the resistant lambs had lower FEC as lactating ewes. Heritability estimate for FEC in peri-parturient ewes was 0.37±0.06, similar to that found in the lambs. Morris et al. (1997) found sheep of the resistant line (low FEC line) to have higher dag scores, which is in contrast to the findings of Bisset et al. (1992). This result likely reflects an immediate hypersensitivity reaction or a heightened immune response mounted by the resistant sheep that may have led to diarrhea (Bisset et al., 1996). Morris et al. (1997) also found that sheep from the resistant line had lower yearling fleece weight and post weaning body weight gains, in contrast to the findings of Bisset et al. (1992) and Albers et al. (1987).

Bishop et al. (1996) also reported genetic variation in response to natural, predominantly *Ostertagia circumcincta* infection in Scottish Blackface lambs. The first FEC was measured when lambs were about 1 mo of age; additional measures were taken monthly until the lambs

were 6 mo of age. Each sampling was followed by an anthelmintic treatment. The first FEC was the result of a primary infection. Heritability estimates for FEC at 1 and 2 mo of age were not significantly different from zero, but heritability increased to 0.22±0.13 by 6 mo of age. The authors indicated that either there may not be any innate resistance to infection or that there is no genetic variation in innate resistance. Genetic correlations between FEC at 3, 4, 5 and 6 mo of age were not significantly different from one and heritability of the average of the four later measurements was 0.33±0.15. The authors suggested that using the average of FEC measures at different ages might be more effective in a breeding program designed to increase resistance.

Woolaston et al. (1992) reported that there was no difference in fecundity of *Haemonchus* maintained for upto 14 generations in lines of sheep that had been selected for increased or decreased resistance to *H. contortus*, suggesting that there was no adaptation of *H. contortus* to genetically resistant sheep. Therefore, it is unlikely that Haemonchus will develop resistance to a genetically resistant sheep for at least 14 parasite generations as it has to various anthelminthics.

Summary

To summarize, resistance to gastro-intestinal nematode infections has a genetic basis that arises mainly from differences in acquired resistance to infection. Young lambs are relatively susceptible and become more resistant as they grow older. After puberty, females appear to be more resistant than males. Animals on a better plane of nutrition are able to cope with effects of infection better. Ewes show a PPR in FEC, possibly because of relaxation of immunity. Breed differences exist in resistance to infection, and subtropical breeds such as St. Croix, Florida Native, and Red Maasai have been shown to be rather resistant. Crossbreeding of susceptible breeds with resistant breeds can result in improvement of resistance of the susceptible breed.

Within-breed variation exists in resistance. Resistance is moderately heritable, and therefore selection for improved resistance is possible. Australian research has indicated that selection based on a single FEC measurement taken at 3 to 5 wk post-infection in previously sensitized sheep might be sufficient to make reasonable genetic progress in reducing FEC. Under Australian conditions, testing on pasture following an artificial infection resulted in similar heritability estimates as testing in pens. New Zealand studies have reported similar heritability estimates as the Australians and have indicated that heritability estimates are highest in slightly older lambs (7 to 8 mo of age). However, they have tended to use a natural rather than an artificial challenge. Scottish studies have indicated that use of the average of 3 to 4 measures of FEC taken at different ages will be most effective in increasing resistance. It is important to measure resistance in sheep after they have had sufficient exposure to parasites to acquire resistance to infection. Therefore, it may not be advisable to attempt to measure resistance in lambs that are less than 3 mo of age. Selection for increased resistance in lambs appears to also confer resistance in peri-parturient ewes, and this has important implications in reducing pasture contamination. Under Australian conditions, production (in terms of body weight) and resistance are favorably correlated. However, fiber diameter and increased resistance are unfavorably correlated and fleece weight and increased resistance have shown conflicting correlations in different studies. Although early New Zealand studies showed favorable relationship of body weight, fleece weight and dag scores with resistance, later studies have indicated no consistent

relationships with body weight but an unfavorable relationship of resistance with fleece weight and dag scores.

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CHAPTER 2

Responses to an artificial *Haemonchs contortus* infection in lambs and ewes. Influence of season, sex of lambs, and age of ewes on resistance

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ABSTRACT: This study describes responses to an artificial *H. contortus* infection in ewes and lambs belonging to a crossbred flock of sheep of 50% Dorset, 25% Rambouillet, and 25% Finnsheep ancestry, and evaluated in spring and fall of 1997 and 1998. Ewes that had dried off after weaning their lambs at about 60 d of age, and lambs that were 120 d of age, were dewormed and infected with approximately 10,000 infective larvae. Ewes were maintained on pasture and lambs were kept in drylot. Body weight (BW, kg), fecal egg count (FEC, eggs/gm), and packed cell volume (PCV, %) were measured at 0, 2, 3, 4, 5, 6 and 7 wk post-infection in lambs and at 0, 3, 5, 7, 9, and 11 wk post-infection in ewes. Ewes and lambs did not lose weight overall in any year or season. Fall-lambing ewes had higher initial PCV and showed earlier declines in FEC than spring-lambing ewes, suggesting limited re-infection in ewes in late winter and early spring. There was no consistent effect of year or lambing season on mean FEC or mean PCV during infection in either ewes or lambs. However, spring-born lambs in 1998 had much lower PCV than other groups of lambs. Generally, yearling ewes appeared to be less resistant to infection with both lower PCV and higher FEC during infection when compared to older ewes. Gains in BW during infection were higher in ram lambs than in ewe lambs, and initial PCV was higher in ewe lambs than in ram lambs. No differences between sexes were observed for FEC or PCV during infection. During infection, PCV was positively correlated with BW and negatively correlated with FEC in both ewes and lambs.

Introduction

Infections with *Haemonchus contortus* are prevalent all over the world and are responsible for economic losses in sheep production (Barger and Cox, 1984). In light of emerging anthelminthic resistance (Overend et al., 1994), there is a need to devise alternative control strategies. One alternative is to breed sheep that are resistant to endo-parasitic infections. Resistance to endo-parasites can be evaluated using responses measured in infected sheep following either artificial challenge (e. g., Albers et al., 1987) or natural pasture challenges (e. g., Bisset et al., 1992).

The experiment described in this paper was designed to measure responses to an artificial *H. contortus* infection in lambs and ewes in order to validate procedures for assessment of parasite resistance in intensively managed sheep. Several other factors affect resistance to internal parasites, including intrinsic factors like age and sex of the sheep, and extrinsic factors like season (Stear and Wakelin, 1998). The objective of this paper is to describe the response of lambs and ewes to an artificial *H. contortus* infection and discuss the effects of sex of lamb, age of ewe, and season on resistance levels.

Materials and Methods

Animals, management and experimental design

Data were collected from lambs and ewes belonging to a crossbred flock of sheep maintained at the Virginia Polytechnic Institute and State University Sheep Center, Blacksburg, Virginia. The sheep were of 50% Dorset, 25% Rambouillet and 25% Finnsheep breeding. This flock was established in the early 1980's (Fossceco and Notter, 1995). In 1988, the animals were subdivided into a fall-lambing flock selected for reduced seasonality in breeding, an unselected fall-lambing environmental control line, and an unselected, spring-lambing genetic control line (Al-Shorepy and Notter, 1996, 1997). Selection continued through the fall 1998 lambing. Lambs for the current study were born in spring (March – April) and fall (late September to early November) of 1997 and 1998 (Table 2.1). Resistance to *H. contortus* was evaluated in both lambs and their dams.

Lambs were creep-fed prior to weaning at approximately 60 d of age and then placed in drylot for a 60-d post-weaning gain test under a standard parasite control regimen. At the end of the gain test, lambs were dewormed with levamisole (using 8 mg/kg orally) and orally dosed with approximately 10,000 infective larvae of *H. contortus* 1 wk later. After infection, lambs were maintained in drylot to prevent re-infection. Fecal samples were collected rectally to estimate the fecal egg counts (FEC), jugular blood samples were collected to estimate packed cell volumes (PCV), and body weights (BW) were also measured at 0, 2, 3, 4, 5, 6, and 7 wk after infection. The BW and PCV were also measured at the time of infection. Thirty-five of 68 spring born lambs in 1997 received a dose of 5,000 infective larvae instead of 10,000 larvae to assess the appropriate dose of larvae for lambs of this size and age. Over the period of the study, four lambs were removed from the study due to low PCV and two were removed due to lameness. In all, 386 lambs sired by 25 sires were evaluated over the 2 yr.

Ewes, aged 1 to 10 yr, were maintained on a standard parasite control program during lactation. Ewes were allowed to dry off after weaning their lambs, dewormed using levamisole, and dosed with approximately 10,000 infective larvae of *H. contortus* 1 wk later. Spring-lambing ewes in yr 1 accidentally received approximately only 5,000 larvae and were dosed with an additional 5,000 larvae 1 mo later. For these ewes, the time of the second dose was treated as the time of infection. Ewes were maintained on pasture and thus may have been re-infected. Body weights, fecal samples to determine FEC, and jugular blood samples to determine PCV were taken at the time of infection and 3, 5, 7, 9 and 11 wk after infection. One spring-lambing ewe died of an unrelated infection in 1997, and two fall-lambing ewes were removed from the study in 1998 because of very low PCV. Fortnightly measurements were taken in ewes because the disease is not as severe as in lambs. A total of 276 ewes (including 78 that were evaluated in both years) by 64 sires were evaluated over the 2 yr.

Fecal egg counts were determined using the modified McMaster's (Whitlock, 1948) technique with each egg representing 50 eggs per gram (epg). Packed cell volumes (%) were determined by the micro-haematocrit centrifuge method.

Data analysis

Data were initially analyzed by analysis of variance using the general linear models procedure of the SAS software package (SAS Inst. Inc., Cary, NC). Data for lambs and ewes were analyzed separately. The model included fixed effects of year, season, either sex (for lambs) or age-category (for ewes), week, all two-way interactions and the three-way interaction for year, season and week. Age categories separated ewes of 1, 2, 3 to 6, or more than 6 yr. Fecal egg counts were not distributed normally. Therefore, a set of logarithmic transformations were applied to FEC and the resulting transformed variables were tested for normality. Normality of residuals was tested using probability plots, skewness and kurtosis values, and the Shapiro-Wilk statistic obtained from a univariate analysis. The most appropriate transformations (LFEC) were ln(FEC + 2000) in lambs and ln(FEC + 25) in ewes. These respective transformations appeared to best normalize FEC in lambs and ewes and were used in all subsequent analyses. One ewe was identified as an outlier because of extremely high fecal egg counts and was removed from the analysis, leaving data from 275 ewes. In a preliminary analysis, the 35 spring-born lambs that received a dose of 5,000 infective larvae in 1997 were found to have significantly lower ($P < 0.01$) mean FEC and LFEC (1,293±192 epg and 8.05±0.44, respectively) than the lambs that were dosed with 10,000 larvae (2,275±202 epg and 8.26±0.44, respectively). Lambs that received 5,000 or 10,000 larvae had similar BW (46.62±0.89 kg and 47.87±0.94 kg, respectively) and PCV (27.76±0.42 % and 27.09±0.43 %, respectively). Lambs that received 5,000 larvae were therefore removed from the analysis**.** Lambs that received 10,000 infective larvae exhibited no apparent ill effects, and 10,000 larvae was taken as the standard dose in future replicates.

Changes in BW, PCV, and LFEC over time were then analyzed by a repeat-measures analysis of variance using the mixed models procedure of SAS software package (SAS Inst. Inc., Cary, NC). For the repeat-measures analysis of LFEC, only data from wk 3 through 7 were used for lambs and only data from wk 3 through 11 were used for ewes. The model used was the same as above but with week as the repeated effect.

The following summary traits were defined for further analysis: initial packed cell volume (IPCV), mean PCV (MPCV), mean BW (MBW), mean FEC (MFEC), and mean log transformed FEC (MLFEC). The MBW was average body weight over all measurement times in both lambs and ewes. The MFEC, MLFEC and MPCV were averaged over the period of infection: wk 3 through 7 in lambs and wk 3 through 11 in ewes. For calculation of summary traits, missing values for BW, LFEC, and PCV were replaced by predicted values derived from a nested analysis of variance including fixed effects of year, season, week, and age-category (for ewes) or sex (for lambs), all two-way interactions, the three-way interaction (year x season x week), and a random effect of animal nested within year, season, and sex (for lambs) or age-category (for ewes). Missing values for PCV were 2% in ewes and 3% in lambs; missing values for FEC were 4% in ewes and 6% in lambs. There were 1% missing values for BW in case of lambs and none in ewes. A nested analysis was used to predict missing values (using PROC GLM of SAS) because the repeat-measures analysis (using PROC MIXED in SAS) does not provide for prediction of missing values. The summary traits were then analyzed using multivariate analysis of variance with year, season, age-category (for ewes) or sex (for lambs),

and their two-way interactions. The summary traits were also used in a later analysis to evaluate genetic control of parasite resistance in these sheep.

Results

Ewes. For the repeat-measures analysis, effects of year, year x age-category interaction, and season x age-category interaction were not significant for any of the traits. Lambing-season did not affect PCV or LFEC. Age-category x week interaction was not significant for BW or LFEC. All other components of the model, including the year x season x week interaction, had a significant effect on all traits, and year x season x week least squares means for BW, PCV and back-transformed LFEC are shown in Fig 2.1. Although there were transient declines in BW between some measurement times, ewes did not lose weight overall in any year or season. Gains were lower in yr 1 (60.33 ± 1.09 kg at wk 0 to 62.10 ± 0.97 kg at wk 11) than in yr 2 (60.56 ± 1.01 kg at wk 0 to 64.51 ± 0.89 at wk 11).

Fall-lambing ewes (October lambing) showed higher initial increase in FEC than spring-lambing (March lambing) ewes. In fall-lambing ewes, FEC initially increased until the 5th wk post-infection and then declined in both years, suggesting limited re-infection of ewes in January and February. In spring-lambing ewes, FEC increased gradually until 9th wk post-infection in yr 2 and increased dramatically after 9th wk post-infection in yr 1. Spring-lambing ewes were possibly exposed to higher infection levels on pasture during June through August, owing to favorable conditions for larval survival during mid-summer and early fall. This could explain the increase in FEC through all measurement times in spring-lambing ewes; however, the dramatic increase in FEC later during infection in yr 1 cannot be explained fully, but could possibly be due to the dosing regimen used for these set of ewes, wherein they received two separate doses of approximately 5,000 larvae at a one month interval. Thus FEC were highly variable over both years and seasons.

The PCV generally declined steadily through at least wk 9 post-infection in all years and seasons, with the exception of a slight increase between wk 3 and wk 5 in spring-lambing ewes of yr 2 and a slight increase between wk 0 and 3 in spring-lambing ewes in yr 1. The PCV continued to decline through wk 11 post-infection in spring-lambing ewes of yr 2, but increased in all other ewe groups. Ewes in yr 2 showed a more rapid decline in PCV. Yearling ewes exhibited a higher ($P < 0.05$) initial and overall decline in PCV compared to ewes of other age-categories and had much higher ($P < 0.05$ to $P < 0.01$) fecal egg counts at all times compared to older ewes (Fig 2.2).

Correlations between adjacent measures ranged from 0.42 to 0.64 for PCV and from 0.34 to 0.76 for LFEC between 3 and 11 wk post-infection (Table 2.2). Correlations between PCV at different times declined as the time between measures increased, with the smallest correlation (0.23) between PCV at wk 0 and 11. Mean values for FEC at wk 0 were consistently small (less than 25 epg) and correlations of LFEC at wk 0 with later measures between LFEC were correspondingly small. Between wk 3 and 11, correlations between LFEC declined as the time between measurements increased but all were 0.39 or larger. Correlations between adjacent measures of BW ranged from 0.95 to 0.97 ($P<0.01$) across all measurement times (data not tabulated).

For the summary traits, yr x age-category and season x age-category interactions did not have a significant effect on any of the traits. Year had a significant effect on only IPCV ($P < 0.05$), and lambing season had a significant effect on IPCV and MBW (both $P < 0.01$). Year x season interaction was significant for MBW, MFEC and MLFEC (Table 2.3, Fig 2.3). Fall-lambing ewes in yr 1 had lower ($P < 0.01$) MBW than all others. Initial PCV was consistently higher in fall-lambing (33.9 ± 0.4 %) than in spring-lambing (30.5 ± 0.5 %) ewes, and was higher in yr 2 (32.8 ± 0.4 %) than in yr 1 (31.5 ± 0.4 %). No consistent effect of year or season on MFEC or MLFEC was observed (Fig 2.3). Spring-lambing ewes in yr 1, and fall-lambing ewes in yr 2, had higher ($P < 0.01$) mean fecal egg counts than the other groups.

Age-category of the ewe had a significant effect on all traits except IPCV (Table 2.4). Yearling ewes had lower ($P<0.05$) MPCV than ewes that were greater than 3 yr of age, and 2-yr-old ewes had lower MPCV than 3 to 6 yr old ewes ($P<0.05$). Yearling ewes had lower MBW ($P< 0.01$) than older ewes, but there were no significant differences for MBW among ewes that were greater than 3 yr of age. Yearling ewes had higher MFEC ($P < 0.05$) and MLFEC ($P < 0.01$) than older ewes, although the difference in MFEC between yearling ewes and ewes that were greater than 6 yr of age was not significant. There were no significant differences between ewes greater than 1 yr of age for MFEC and MLFEC.

Correlations among summary traits are shown in Table 2.5. Initial PCV and MPCV were positively correlated with each other and with MBW and were negatively correlated with MFEC and MLFEC, although the correlation between IPCV and MLFEC was not significant. Mean BW was not correlated with fecal egg count measures. Mean FEC and MLFEC were positively correlated. Higher fecal eggs counts were thus associated with lower packed cell volumes during infection but did not affect body weight in ewes in this study.

Lambs. For the repeat-measures analysis, effects of year x season x week interaction were significant ($P<0.01$) for all traits. Effects of sex x yr and sex x season interactions were not significant ($P>0.05$) for any of the traits and sex x wk interaction was not significant ($P>0.05$) for PCV and LFEC. Effects of yr, season, and sex were not significant ($P>0.05$) for LFEC. Year x season x week least squares means for BW, PCV, and back-transformed LFEC are shown in Fig 2.4. Lambs continued to grow during infection. Spring-born lambs in yr 1 were much heavier than the others and experienced a transient decline in BW at 5th wk post-infection. The FEC increased by 3rd wk post-infection and then remained high but were erratic in different yr and seasons. Fall-born lambs in yr 1 and spring-born lambs in yr 2 had much higher FEC than spring-born lambs in yr 1 or fall-born lambs in yr 2. The PCV decreased almost linearly until 3rd wk post-infection and thereafter remained relatively low and stable. Spring-born lambs in yr 2 had much lower PCV than other groups. The BW gains during infection were higher ($P < 0.01$) in ram lambs (38.5 ± 0.5 kg at wk 0 to 48.9 ± 0.6 kg at wk 7) than in ewe lambs (33.8 ± 0.5 kg at wk 0 to 41.5 ± 0.6 kg at wk 7).

Correlations between adjacent measures ranged from 0.53 to 0.76 for PCV, and were highest for LFEC between 3 and 7 wk post-infection, ranging from 0.29 to 0.58 (Table 2.6). Correlations involving PCV in lambs declined less rapidly over time than those observed in ewes (Table 2.2). As in ewes, the very low mean values for LFEC at wk 0 and 2 (less than 100 epg) were associated with low correlations with LFEC at later times. Correlations between adjacent

measures of LFEC were highest at the peak of infection, between 3 and 5 wk post-infection. Correlations between adjacent measures of BW ranged from 0.95 to 0.97 ($P<0.01$) across all measurement times (data not tabulated).

For summary traits, effects of yr x season interaction were significant ($P<0.01$) for all traits except IPCV. Effects of yr x sex and season x sex were not significant ($P>0.05$) for any of the traits. Yr and season did not have significant ($P>0.05$) effects on IPCV, MFEC, or MLFEC. Mean PCV was lowest in spring-born lambs of yr 2 (22.4 ± 0.4 %) and MBW was highest in spring-born lambs of yr 1 (46.3 ± 1.2 kg). Yr x season least square means for MFEC and back-transformed MLFEC are shown in Fig 2.3. Spring-born lambs in yr 2 and fall-born lambs in yr 1 had higher ($P < 0.01$) fecal egg counts than the other groups. No consistent effect of year or season on MFEC or MLFEC was observed (Fig 2.3). Sex of lamb affected only IPCV ($P < 0.05$) and MBW ($P < 0.01$). Initial PCV was higher in ewe lambs (33.2 ± 0.2 %) than in ram lambs (32.5 ± 0.2 %), and ram lambs were 6.3 kg heavier than ewe lambs ($P < 0.01$).

Correlations among summary traits are given in Table 2.5. Initial PCV was positively correlated with MBW and MPCV, but was not associated with measures of FEC. Mean PCV was positively correlated with MBW and negatively correlated with measures of FEC. Mean BW was negatively correlated with FEC measures. Mean FEC and MLFEC were strongly positively correlated with each other. Thus, in lambs, higher fecal egg counts were associated with lower packed cell volumes and body weights during infection.

Discussion

Ewes did not lose weight and lambs continued to grow throughout the measurement period, indicating no major negative effects of infection on body weight in this production environment. There was a seasonal variation in patterns of FEC over time in ewes. Generally, fall-lambing ewes showed an early increase in FEC whereas spring-lambing ewes showed a later increase in FEC, presumably associated with re-infection in spring-lambing ewes grazing contaminated pastures during summer. No clear differences between seasons were observed for lambs, and they were much more variable in response to infection over time in different years and seasons.

Adult ewes are relatively more resistant to infection than lambs. This was evident in our study as ewes generally had higher PCV and lower FEC during infection in spite of being continually re-infected. Adult sheep may be able to control both worm burdens and worm fecundity as a result of a better acquired immune response, whereas lambs appear to be able to regulate only worm fecundity (Stear et al. 1999). Age affects resistance to infection in lambs, with older lambs being more resistant (Gamble and Zajac, 1992; Kambara et al., 1993). In this study, age appeared to affect resistance of ewes; yearling ewes were less resistant to infection than older ewes. Yearling ewes had higher mean FEC, a steeper decline in PCV, and lower PCV at all post-infection measurement times compared to older ewes; 2-yr-old ewes were intermediate in PCV. In an early study, Gregory et al. (1937) compared adult ewes of different ages and found that younger ewes were more susceptible than older ewes, but that after 2 yr of age, resistance to parasitic infections was not affected by age.

Seasonal variation in FEC has been reported in previous studies of natural infection on pastures (Tembely et al., 1998; Doligalska et al., 1997). Fecal egg counts in spring are usually high. In this study, although there was variation in FEC between seasons within each year, there was no consistent seasonal variation in FEC over the years in either ewes or lambs. In one year, FEC were higher in fall whereas in the other FEC were higher in spring. Seasonal variation in FEC is most likely dependent on variation in availability of infective larvae on pastures. Two peaks in FEC can be seen: one during early- to mid-spring due to development of over-wintered larvae, and another in mid-summer or early fall depending on weather conditions (Gregory et al., 1940; Whittier et al., 1997). Since lambs were not on pasture and were kept in drylot after infection, seasonal variation in FEC due to availability of infective larvae on pastures was unlikely to be seen in lambs in this study. Generally, initial PCV was higher in fall-born lambs and fall-lambing ewes.

Sex of lambs has been reported to affect resistance to parasitic infections. Females are more resistant to infection and have lower FEC than males after puberty, although there appear to be no differences between sexes prior to puberty (Courtney et al., 1985; reviewed by Barger, 1993; Woolaston and Piper, 1996). Our results with these pre-pubertal lambs are thus consistent with earlier reports.

Conclusions

The testing protocol used in this study will not adversely affect growth and condition of sheep and will allow adequate measurement of FEC and PCV for testing resistance of sheep to *H. contoruts*. There was no consistent seasonal variation in FEC. Younger ewes were more susceptible to infection than older ewes, but sex differences in fecal egg counts were not observed in these pre-pubertal lambs.

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Table 2.1 Numbers of spring- and fall-lambing ewes and their lambs evaluated in each year.

	No. of:	
Year and Season	Ewes	Lambs (Female + Male)
Spring 1997	40	33 (20 + 13)
Fall 1997	103	157 (77 + 80)
Spring 1998	41[a]	64 (27 + 37)
Fall 1998	91[b]	132 (63 + 69)
Total	275	386 (187+199)

[a] 30 of these repeated from spring 1997.
[b] 48 of these repeated from fall 1997.

Table 2.2 Correlations between measures of log transformed fecal egg count (above the diagonal) and packed cell volume (below the diagonal) in ewes facing an artificial *H. contortus* infection.

	Post-infection measurement at:					
	wk 0	wk 3	wk 5	wk 7	wk 9	wk 11
wk 0		0.34 **	0.13 †	0.12 †	0.14 †	0.15 †
wk 3	0.60 **		0.54 **	0.48 **	0.49 **	0.39 **
wk 5	0.42 **	0.58 **		0.61 **	0.56 **	0.42 **
wk 7	0.41 **	0.58 **	0.64 **		0.63 **	0.54 **
wk 9	0.33 **	0.42 **	0.43 **	0.58 **		0.76 **
wk 11	0.23 **	0.30 **	0.29 **	0.36 **	0.42 **	

** $P < 0.01$.
* $P < 0.05$.
† $P < 0.10$.

Table 2.3 Yr x season least square means (± SE) for initial packed cell volume (IPCV, %), mean packed cell volume (MPCV, %), and mean body weight (MBW, kg) in spring- and fall-lambing ewes, and spring- and fall-born lambs, facing an artificial *H. contortus* challenge, across the 2 yr.

Year, season	Trait[a]		
	IPCV	MPCV	MBW
Ewes:			
Yr1, fall-lambing	32.8 ± 0.5	28.1 ± 0.4	57.2 ± 1.3
Yr1, spring-lambing	30.3 ± 0.6	28.8 ± 0.5	65.9 ± 1.4
Yr2, fall-lambing	34.9 ± 0.5	28.6 ± 0.4	62.5 ± 1.1
Yr2, spring-lambing	30.6 ± 0.6	27.9 ± 0.5	63.4 ± 1.4
Lambs:			
Yr1, fall-born	33.4 ± 0.2	26.3 ± 0.2	40.1 ± 0.5
Yr1, spring-born	32.3 ± 0.5	27.1 ± 0.5	46.3 ± 1.2
Yr2, fall-born	32.9 ± 0.2	26.5 ± 0.3	40.3 ± 0.6
Yr2, spring-born	32.8 ± 0.3	22.4 ± 0.4	39.6 ± 0.8

[a] Initial PCV was measured at the time of infection; MBW is the average of body weight measures across all measurement times; and MPCV is the average of fortnightly measurements taken 3 through 11 wk post-infection in ewes, and weekly measurements taken 3 through 7 wk post-infection in lambs.

Table 2.4 Least square means (± SE) for initial packed cell volume (IPCV, %), mean packed cell volume (MPCV, %), mean body weight (MBW, kg), mean fecal egg count (MFEC, eggs/gm), and back-transformed mean log fecal egg count (MLFEC, eggs/gm) for different age categories in ewes facing an artificial *H. contortus* challenge.

Age-category	Trait[a]				
	IPCV	MPCV	MBW	MFEC	MLFEC
1 yr	32.5 ± 0.8	27.1 ± 0.7	51.6 ± 1.9	1264 ± 254	319 ± 86
2 yr	32.0 ± 0.5	28.3 ± 0.4	61.9 ± 1.2	575 ± 161	118 ± 20
3 – 6 yr	32.6 ± 0.3	29.3 ± 0.2	68.9 ± 0.7	476 ± 91	87 ± 9
> 6 yr	31.6 ± 0.6	28.7 ± 0.5	66.3 ± 1.4	779 ± 183	83 ± 16

[a] Initial PCV was measured at the time of infection; MBW is the average of body weight measures across all measurement times; and MPCV, MFEC, and MLFEC are averages of measurements taken 3 through 11 wk post-infection.

Table 2.5 Correlations among initial packed cell volume (IPCV), mean packed cell volume (MPCV), mean body weight (MBW), mean fecal egg counts (MFEC), and mean log fecal egg counts (MLFEC) in ewes (above the diagonal) and lambs (below the diagonal) facing an artificial *H. contortus* challenge.

	Traits [a]				
	IPCV	MPCV	MBW	MFEC	MLFEC
IPCV		0.69 **	0.35**	-0.13 *	-0.10
MPCV	0.39 **		0.29 **	-0.45 **	-0.39 **
MBW	0.20 **	0.26 **		0.06	0.08
MFEC	-0.07	-0.62 **	-0.21 **		0.74 **
MLFEC	-0.09	-0.65 **	-0.20 **	0.94 **	

[a] MBW is the average of body weight measures across all measurement times; IPCV was measured at time of challenge; MPCV, MFEC and MLFEC are averages of measurements taken at 3 through 11 wk post-infection in ewes and at 3 through 7 wk post-infection in lambs.
* $P < 0.05$.
** $P < 0.01$.

Table 2.6 Correlations between measures of log transformed fecal egg count (above the diagonal) and packed cell volume (below the diagonal) in lambs facing an artificial *H. contortus* infection.

	Post-infection measurement at:						
	wk 0	wk 2	wk 3	wk 4	wk 5	wk 6	wk 7
wk 0		0.06	0.01	-0.02	0.09	0.06	-0.10
wk 2	0.53 **		-0.11	0.04	0.03	0.24 **	0.24 **
wk 3	0.42 **	0.63 **		0.58 **	0.43 **	0.19 **	0.34 **
wk 4	0.38 **	0.51 **	0.63 **		0.51 **	0.19 **	0.42 **
wk 5	0.35 **	0.48 **	0.64 **	0.67 **		0.29 **	0.42 **
wk 6	0.34 **	0.41 **	0.52 **	0.65 **	0.69 **		0.29 **
wk 7	0.34 **	0.47 **	0.58 **	0.66 **	0.73 **	0.76 **	

** $P < 0.01$.

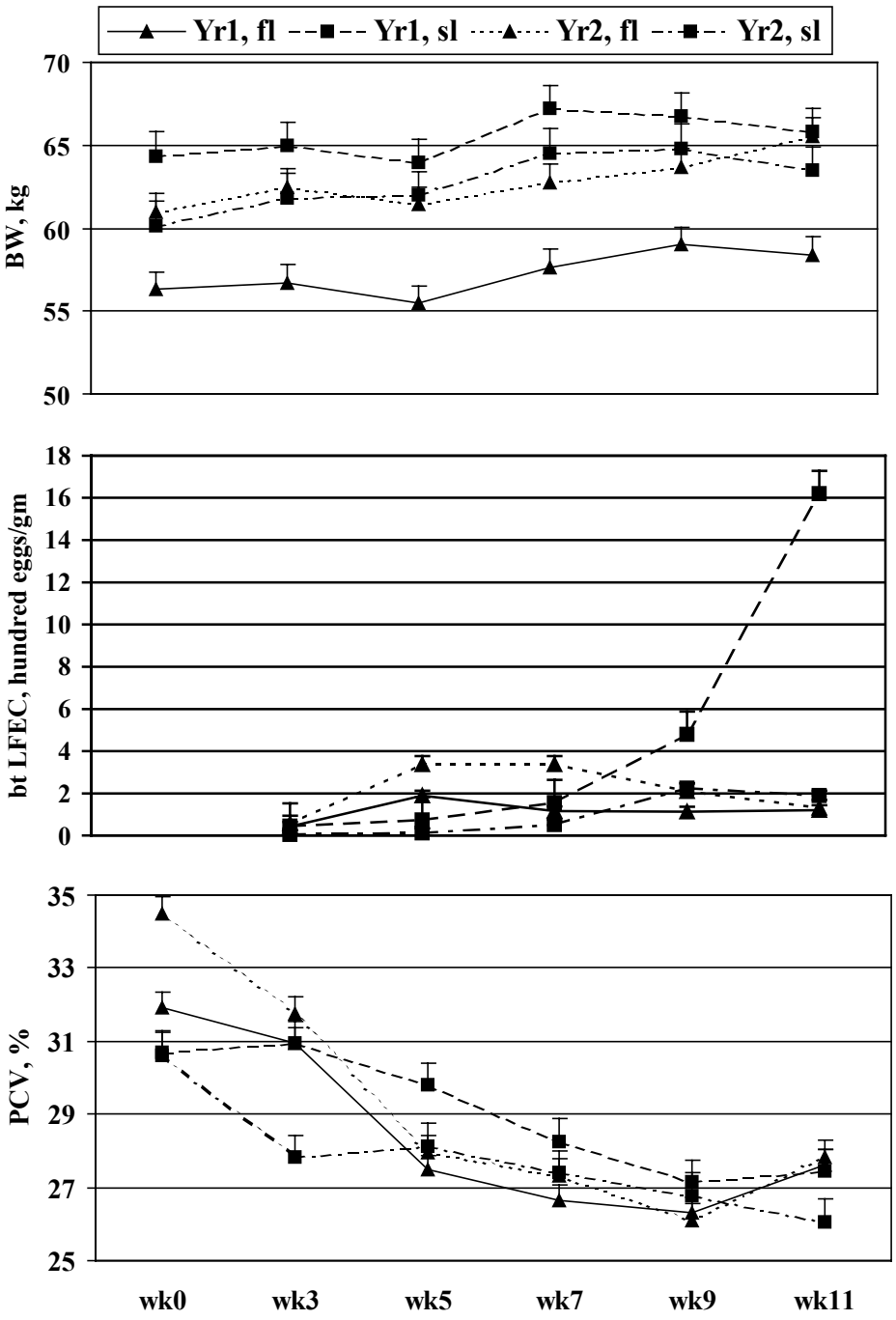

Fig 2.1 Year x season x week least square means over measurement times for body weight (BW; kg), back-transformed log fecal egg counts (bt LFEC; eggs/gm), and packed cell volume (PCV; %) in ewes facing an artificial *H. contortus* challenge.

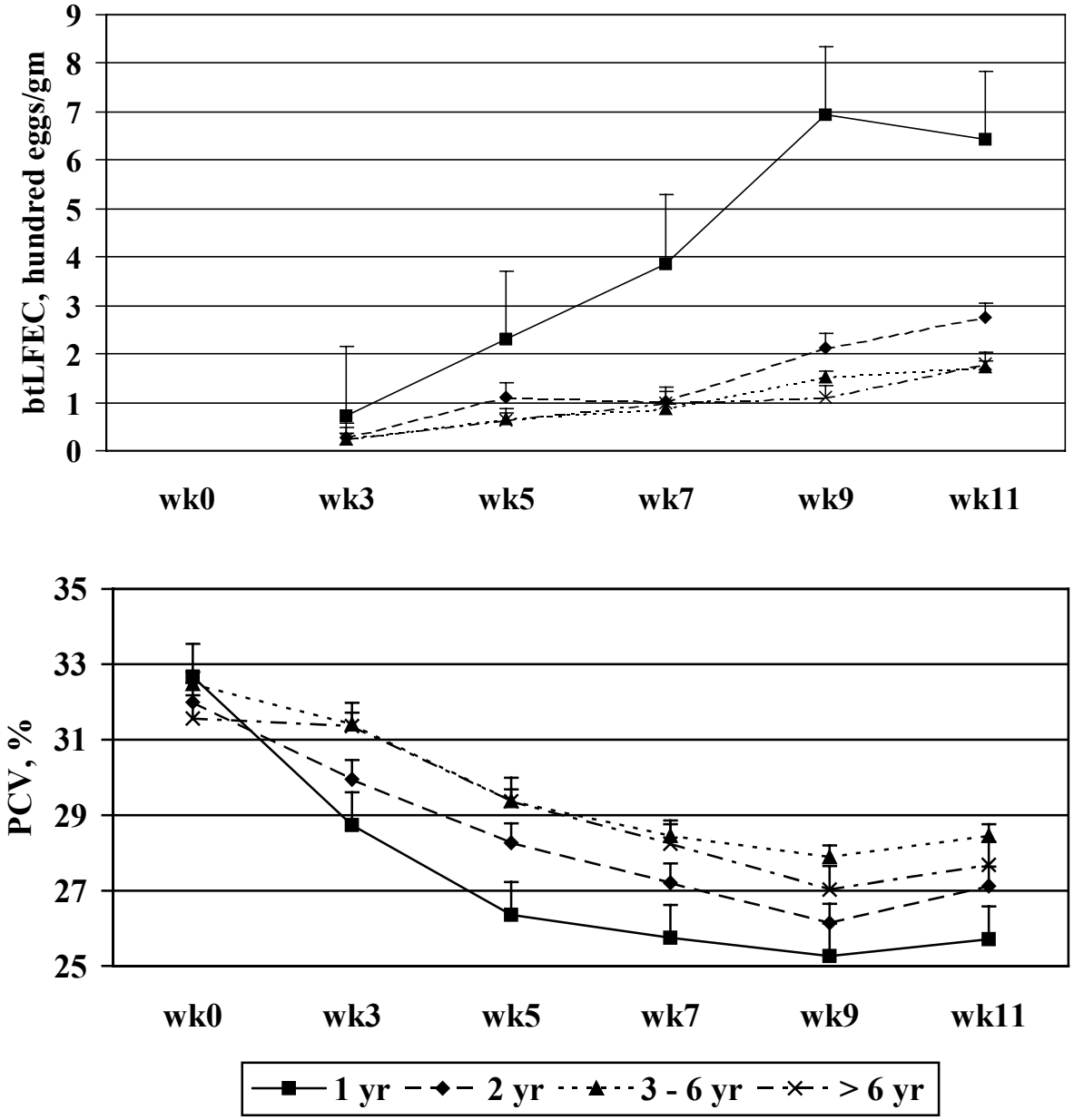

Fig 2.2 Age-category x wk least square means over measurement times for back-transformed log fecal egg count (btLFEC) and packed cell volume (PCV, %) in ewes facing an artificial *H. contortus* infection. Age categories separated ewes of 1, 2, 3 to 6, and greater than 6 yr in age.

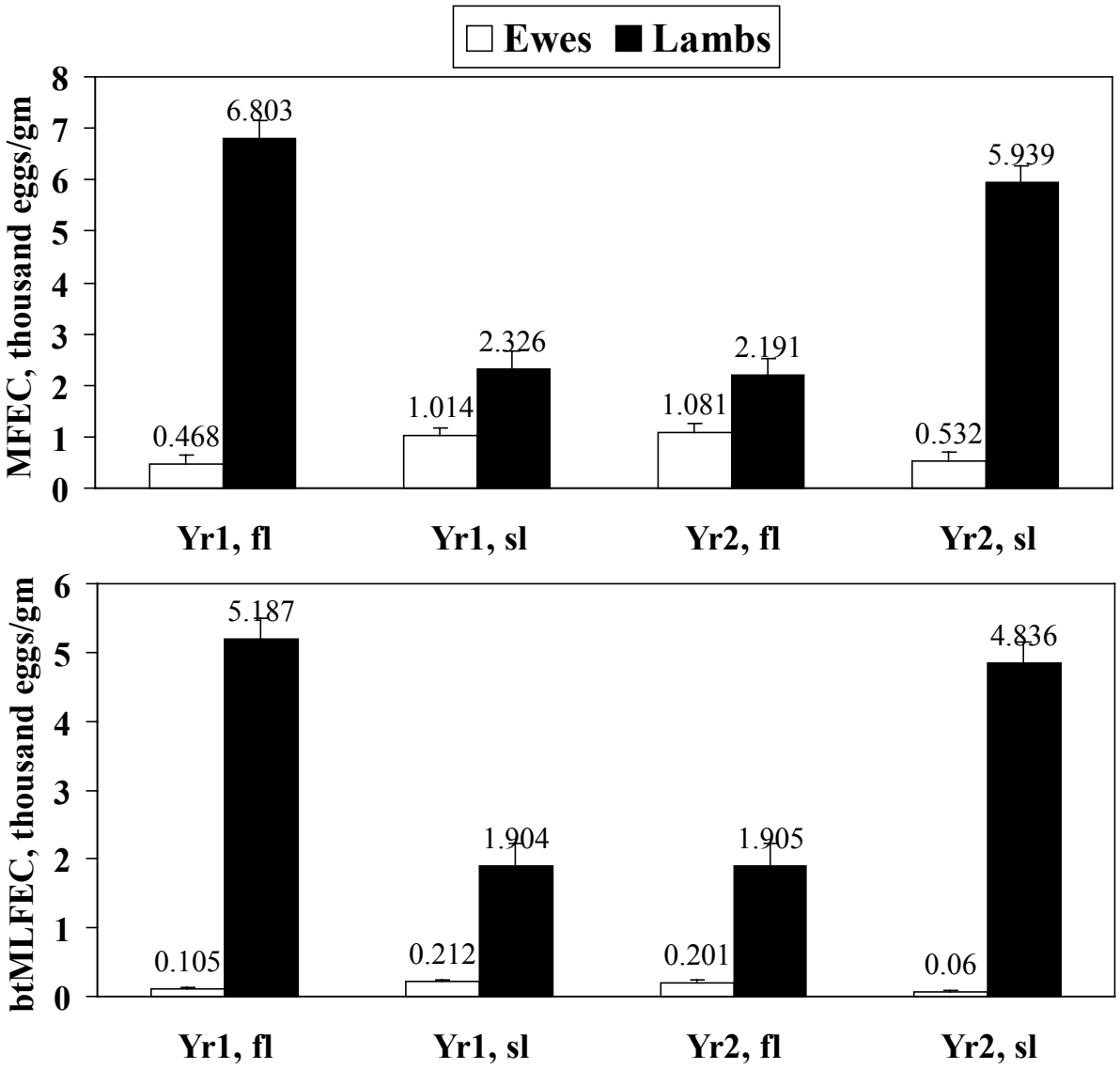

Fig 2.3 Yr x season least square means for mean fecal egg counts (MFEC, eggs/gm) and back-transformed mean log fecal egg counts (bt MLFEC, eggs/gm) in spring- and fall-lambing ewes, and spring- and fall-born lambs, facing an artificial *H. contortus* challenge, across the 2 yr.

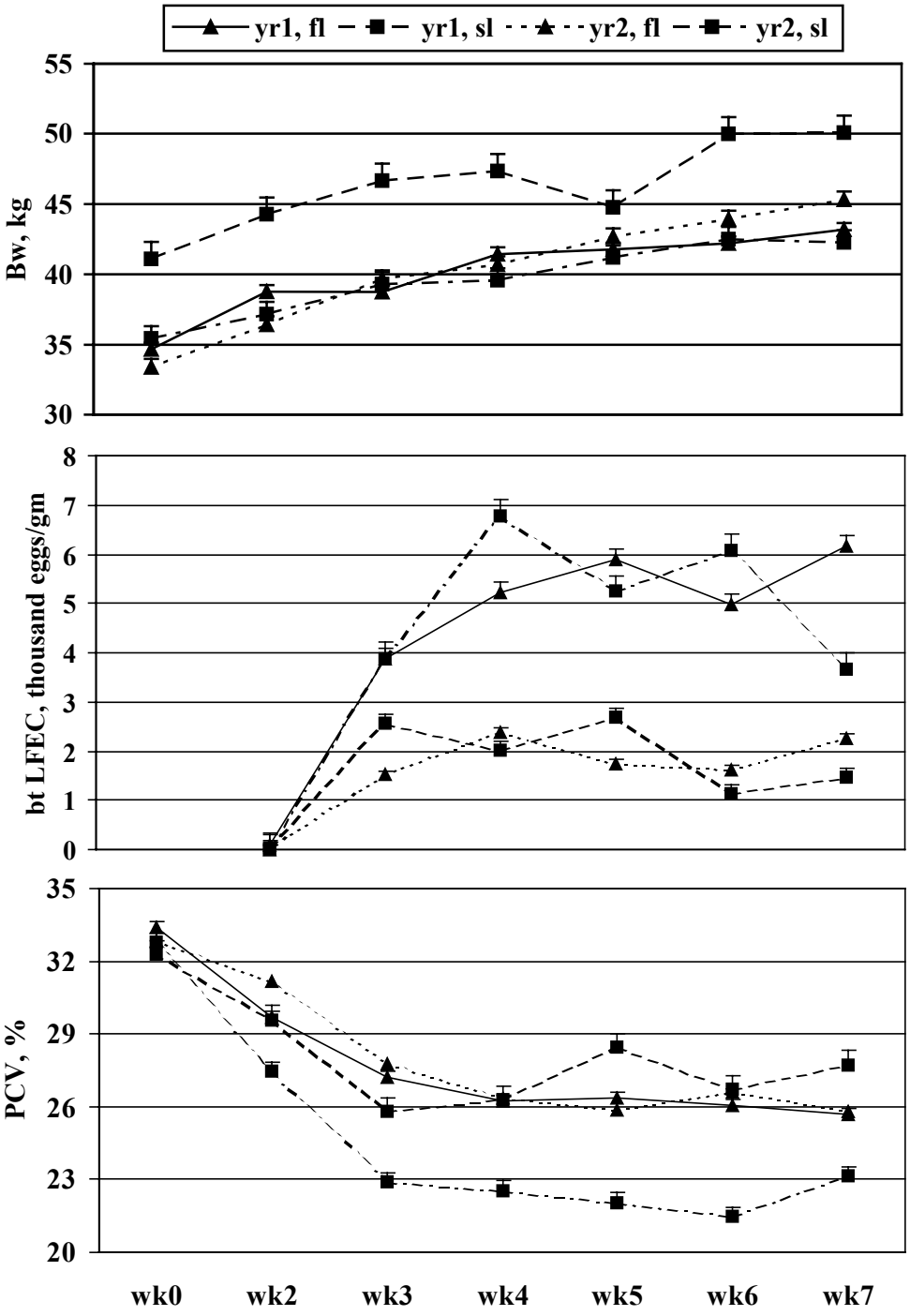

Fig 2.4 Yr x season x wk least square means over measurement times for body weight (BW, kg), back-transformed log fecal egg counts (btLFEC [a], eggs/gm), and packed cell volume (PCV, %) in lambs facing an artificial *H. contortus* infection.
[a] Least square means for btLFEC at wk 2 were obtained from a separate analysis.

CHAPTER 3

Inheritance of fecal egg count, packed cell volume, and body weight, and their relationship with production traits in sheep infected with *Haemonchus contortus*

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ABSTRACT: This study assessed genetic control of resistance to *H. contortus* in sheep of 50% Dorset, 25% Rambouillet and 25% Finnsheep breeding. A total of 198 ewes out of 64 sires and 386 lambs out of 25 sires were evaluated in fall and spring over 2 yr. Lambs were dewormed at about 120 d of age and ewes were dewormed shortly after weaning their lambs. One wk later, ewes and lambs were infected with approximately 10,000 infective larvae. Lambs were maintained in drylot; ewes were maintained on pasture. After infection, body weight (BW), fecal egg counts (FEC) and packed cell volume (PCV) were measured weekly for 7 wk in lambs and fortnightly for 11 wk in ewes. Summary traits were defined as initial PCV, mean BW across all times, and means for FEC (MFEC), log-transformed FEC (MLFEC), and PCV (MPCV) at wk 3 through 7 post-infection for lambs and wk 3 through 11 post-infection for ewes. All traits were moderately heritable in both ewes and lambs. Heritability of MLFEC was 0.27 ($P<0.01$) in lambs and 0.55 ($P<0.01$) in ewes. Heritability of MPCV was 0.57 ($P<0.01$) in lambs and 0.25 ($P<0.01$) in ewes. Between-year repeatabilities were moderate for all summary traits in ewes. Correlations between dam and lamb records for MFEC and MLFEC were generally low, suggesting different mechanisms of resistance in lambs and ewes. Ewes with a higher genetic merit for growth as lambs were less resistant to infection as adults, but genetic merit for fertility and prolificacy were not related to parasite resistance. Lambs with improved genetic merit for body weight were clearly not more susceptible to infection. Thus, response to *H. contortus* is heritable, and selection for resistance is possible and will not adversely affect growth of lambs and fertility of ewes in this production environment.

Introduction

Gastro-intestinal helminth infections adversely affect the sheep industry through production losses, treatment and management costs, and mortality of sheep. Increasing incidence of anthelminthic resistance (Overend et al., 1994), and growing demand for animal products that are produced without the use of chemical substances (i.e. 'organically' produced), have prompted a search for alternative methods for controlling helminthiasis in sheep. Over the past several years, evidence has emerged that suggests a genetic basis for resistance to gastro-intestinal nematodes in sheep. There have been reports of both genetic differences among breeds (Courtney et al., 1985; Baker et al., 1999) and within-breed variation in resistance to infection by gastro-intestinal helminthes. Moderate heritabilities have been reported for resistance to *Haemonchus contortus* in the Australian Merino (Woolaston and Piper, 1996), *Trichostrongylus colubriformis* in New Zealand Romneys (Bisset et al., 1992) and *Ostertagia ostertagi* in Scottish Blackface sheep (Bishop et al., 1996). Heamonchus infections are prevalent in several parts of the United States and early North American studies documented within-breed variation in

response to helminth infection (Scrivner, 1967); however, there have not been any published reports of genetic parameter estimates for parasite resistance traits in sheep in the US.

The objectives of this paper were to estimate the heritability and repeatability of fecal egg count (FEC) and packed cell volume (PCV) in lambs and ewes following an artificial infection with *H. contortus* larvae, to estimate correlations among FEC, PCV and body weight (BW) of lambs and ewes, and to investigate relationships between measures of parasite resistance and genetic merit for production traits.

Materials and Methods

Animals, management and experimental design

Details of the experimental procedure are described in Chapter 2. Briefly, data were collected from lambs and their dams in a crossbred flock of 50% Dorset, 25% Rambouillet and 25% Finnsheep breeding maintained at the Virginia Polytechnic Institute and State University's Sheep Center, Blacksburg, Virginia. This flock was established in the early 1980's (Fossceco and Notter, 1995) and in 1988 was subdivided into a fall-lambing flock selected for reduced seasonality in breeding, an unselected fall-lambing environmental control line, and an unselected, spring-lambing genetic control line (Al-Shorepy and Notter, 1996, 1997). Selection continued through the fall 1998 lambing. Lambs for the current study were born in spring (March – April) and fall (late September to early November) of 1997 and 1998.

Lambs were weaned at approximately 60 d of age and then placed on a 60-d post-weaning gain test under a standard parasite control regimen. Lambs were dewormed with levamisole at about 120 d of age, orally dosed with 10,000 infective larvae of *Haemonchus contortus* 1 wk later, and thereafter maintained in a drylot. Fecal samples and jugular blood samples were collected at the time of infection and 2, 3, 4, 5, 6, and 7 wk post infection. Body weight (BW) was also measured at these times. In all, 386 lambs sired by 25 sires were evaluated over the 2 yr.

Ewes, aged 1 to 10 yr, were maintained on a standard parasite control program during lactation and allowed to dry off after weaning their lambs. They were then dewormed using levamisole, and dosed with 10,000 infective larvae of *H. contortus* 1 wk later, and subsequently maintained on pasture. Fecal samples and jugular blood samples were taken at the time of infection and 3, 5, 7, 9 and 11 wk after infection. Body weight was also measured at these times. Fortnightly measurements were taken in ewes because the disease is not as severe as in lambs. A total of 198 ewes by 64 sires were evaluated over the 2 yr; 78 ewes were evaluated in both years, giving a total of 276 ewe records.

Fecal egg counts (FEC) were determined using the modified McMaster's technique (Whitlock, 1948) with each egg count equal to 50 eggs per gram. Packed cell volumes (PCV; %) were determined by the micro-haematocrit method.

Data analysis

Data were initially analyzed by analysis of variance using the general linear models procedure of the SAS software package (SAS Inst. Inc., Cary, NC). For lambs, the model included fixed effects of year, season, week, sex, all two-way interactions and the three-way interaction for year, season, and week. Fecal egg counts were not distributed normally and were transformed to ln(FEC + 2000) (LFEC) for further analysis. Five lambs were not found in the pedigree records and were removed from the genetic analysis, leaving data from 381 lambs. For ewes, the model included effects of year, season, week, age category, all two-way interactions, and the three-way interaction for year, season, and week. Age categories separated ewes of 1, 2, 3 to 6, or more than 6 yr. The FEC were transformed to ln(FEC + 25) in ewes. One ewe record was identified as an outlier because of extremely high fecal egg counts and one ewe was not found in pedigree records; these animals were removed from the dataset, leaving data from 196 ewes (274 ewe records) for genetic analysis. The following composite traits were defined for use in the genetic analysis: initial packed cell volume (IPCV), mean BW (MBW), mean FEC (MFEC), mean log transformed FEC (MLFEC), and mean PCV (MPCV). The MBW was average of body weights over all measurement times in both lambs and ewes. The MFEC, MLFEC and MPCV were averaged over the period of infection: wk 3 through 7 in lambs and wk 3 through 11 in ewes.

Heritabilities in both lambs and ewes, and between-year repeatabilities in ewes, were estimated for composite measures of resistance in a single-trait analysis using restricted maximum likelihood (REML; Boldman et al., 1993). The model fitted included fixed effects of year, season, and either sex (for lambs) or age category (for ewes), and random animal additive effects and permanent environment effect (for ewes only). Heritability of individual measures of PCV, FEC and LFEC during infection was also estimated separately at each measurement time using the same model or across times using the above-mentioned model with the addition of week as a fixed effect and a permanent environment effect for lambs or ewes. Tests of significance for heritability were done using likelihood ratio tests after deleting the random animal additive effect from the full model. Seventy-eight ewes were evaluated in both years and used to derive repeatability estimates.

Several other statistics were calculated to provide additional information regarding the genetic basis for parasite resistance and the association of resistance with genetic merit for other production traits. Correlations between records of lambs and their dams were obtained using multi-variate analysis of variance after additive adjustment for the age category of the ewe and sex of the lambs. Records of ewes with more than one lamb in the study were repeated for each lamb. Correlations between records of twin lambs (123 sets of twins) were obtained after adjusting for the sex of the lamb.

Estimated breeding values (EBV) for all animals in these flocks were available for the following production traits: birth weight (BWT), maternal birth weight (MBWT), weaning weight (WW), maternal weaning weight (MWW), 120-d post-weaning weight (PWW), fertility in autumn lambing (FF), and number of lambs born per 100 ewes lambing (NB). Associations between EBV for each production trait and composite measures of parasite resistance were

estimated using regression analyses. Each analysis included fixed effects of year, season, year by season interaction, and sex (for lambs) and age category (for ewes) and one of the EBV. Additionally, the actual initial BW (IBW) was fitted as a second covariate in regression analyses involving WW and PWW for ewes and lambs to attempt to distinguish genetic and phenotypic relationships. Residual correlations between IBW and WW EBV were 0.54 ($P<0.01$) and 0.47 ($P<0.01$) in lambs and ewes, respectively. Residual correlations between IBW and PWW EBV were 0.55 ($P<0.01$) and 0.48 ($P<0.01$) in lambs and ewes, respectively.

Results and Discussion

Overall means for the composite traits are given in Table 3.1. As expected, FEC was higher and PCV lower during infection in lambs than in ewes. Lambs are generally considered to be susceptible to infection until about 1 yr of age and become increasingly less susceptible as they grow older (Courtney et al., 1985). Adult ewes are relatively resistant to infection except during late pregnancy and lactation (Courtney et al., 1984).

Genetic parameter estimates for parasite resistance traits from the REML analyses are shown in Table 3.2. All the traits in lambs were moderately to highly heritable. The MBW was highly heritable. Heritability of MPCV was higher than that of IPCV, in part because averaging PCV measures across times reduces phenotypic variance and thus increases the heritability. Repeatability of PCV across times in lambs was 0.66 ($P < 0.01$), and heritabilities of individual PCV measures taken during the infection ranged from 0.24 to 0.54 ($P < 0.01$; not tabulated). Hence, the heritability of IPCV was similar to that observed for individual measures of PCV during infection. Albers et al. (1987) reported heritabilities of 0.45 and 0.35 for individual PCV measurements taken 4 and 5 wk post-infection, respectively, in young lambs. These estimates are similar to the heritability of IPCV and also to that of individual PCV measures taken during infection. Similarly in ewes, the heritability of IPCV was lower than that for MPCV. However, heritability estimates for individual PCV measurements in ewes during infection ranged from 0.14 to 0.24 (not tabulated) and were thus similar to that of IPCV. Repeatability of PCV across measurement times was 0.48 in ewes ($P< 0.01$). Heritabilities of individual PCV measurements during infection were much lower in ewes than those estimated for lambs in this study. In both ewes and lambs, average PCV during infection appears to be a better selection criterion for improving resistance to *H. contortus* because of the modest repeatability of PCV across sampling times and the associated increase in heritability of mean PCV.

Heritability of MFEC and MLFEC were moderate in lambs and the estimate is similar to those reported for *H. contortus* (Albers et al., 1987) and *T. colubriformis* (Bisset et al., 1992; Woolaston and Windon, 2001) infections. Albers et al. (1987) reported heritability estimates for FEC and PCV to be 0.3±0.1 and 0.4±0.1 respectively. Log transformation only slightly increased the heritability of mean FEC in lambs. Woolaston and Piper (1996) have reported a heritability of 0.23 for untransformed FEC in case of an artificial *H. contortus* infection in 5 to 6 mo old Merino lambs. In the current study, repeatabilities of FEC and LFEC across all measurement times were 0.36 ($P <0.01$) and 0.40 ($P <0.01$), respectively, and heritabilities of fecal egg counts were higher at 3, 4 and 5 wk post-infection (0.46, 0.15, and 0.43, respectively for FEC; 0.42, 0.22, and 0.25, respectively for LFEC; $P<0.01$) than at 6 and 7 wk post-infection (0.05 and 0.04 for FEC; 0.07 and 0.05 for LFEC; not significant). Morris et al. (1997) reported

heritabilities for individual FEC to range from 0.29 to 0.42 in Romneys facing natural mixed challenges on pasture, with highest heritability recorded at 7 to 8 mo of age. Barger and Dash (1987) have reported a repeatability of 0.56 for LFEC during an extended *H. contortus* infection in lambs. In this study, heritabilities of FEC and LFEC taken at 3 through 5 wk post-infection were 0.26 and 0.25, respectively (both P<0.01) and repeatabilities across wk 3, 4 and 5 wk post-infection for FEC and LFEC were 0.48 and 0.52, respectively (both P<0.01). Thus, the expectation of heritability for the mean of three measurements taken 3 through 5 wk post-infection in lambs were 0.39 and 0.38 for FEC and LFEC, respectively, which are similar to the heritability for mean FEC (0.39, P<0.01) and mean LFEC (0.37, P<0.01) averaged over wk 3 through 5. It appears that the use of an average measure of FEC across all measurement times did not improve the heritability compared to using an average measure of FEC across 3 through 5 wk after infection in lambs. It also appears from this study that an average measure of FEC at the peak of infection (3 through 5 wk post-infection) was not more heritable than a single measure of FEC taken at 3 wk post-infection. Woolaston and Windon (2001) suggested use of one FEC measure between 3 and 5 wk post-infection for reduction of FEC in *T. colubriformis* infections in young Merinos. In contrast, Bishop et al. (1996) suggest use of the average of three to four FEC measures to improve resistance to *Ostertagia circumcincta* infection in young lambs.

In ewes, heritability of MFEC was not significantly different from 0 and most of the individual FEC measures were not heritable (range of 0 to 0.19; not significant). However, log transformation increased heritability to 0.55 (P<0.01), which was considerably higher than the heritability of MLFEC in lambs. Repeatabilities of FEC and LFEC across times were 0.34 (P<0.01) and 0.43 (P<0.01), respectively, and individual heritability measures for LFEC in ewes were moderate at 3, 5, 7, 9 and 11 wk after infection (0.16, 0.25 (P < 0.10), 0.41 (P<0.01), 0.37 (P < 0.01), and 0.26 (P < 0.01), respectively). Unlike in lambs, the FEC were more heritable during the later part of infection than early in infection in ewes. The heritability of LFEC in lactating ewes measured at 4 and 6 wk after lambing was found to be 0.23 by Bishop and Stear (2001). This value is somewhat lower than those obtained here, but infection in dry ewes is different from that in lactating ewes, and the study by Bishop and Stear involved animals facing a mixed natural infection on pasture.

Repeatabilities of IPCV, MPCV, MFEC and MLFEC across years in ewes (Table 3.2) were moderate to high. The between-year repeatability of 0.56 for MLFEC and also the repeatability of 0.43 across times for LFEC was higher than the value of 0.25 obtained by Bishop and Stear (2001) for two LFEC measures taken at 4 and 6 wk post-lambing over a 4-year period in lactating ewes.

Correlations between records of dams and lambs and between records of twin lambs are shown in Table 3.3. Correlations between records of dams and lambs were generally very low and not significantly different from 0 for FEC or LFEC. This suggests that the responses to infection in lambs and non-lactating ewes are not the same trait, in support of the very different heritabilities for the traits in lambs and ewes. Courtney et al. (1986) suggested that selection for reduced PPR in ewes might not improve resistance in the progeny because the correlation between FEC of dams and their ewe lambs was not significant. They suggested that acquired resistance in young lambs and PPR in ewes are controlled by different genetic mechanisms.

Lambs appear to be resistant by being able to control worm growth and fecundity rather than worm numbers, whereas older sheep can control both and therefore have much lower FEC than lambs (Stear et al., 1999). However, there have been earlier reports which indicate that selection of lambs for increased resistance to parasitic infection also confers some degree of resistance in the peri-parturient ewe (Morris et al., 1998). Windon and Dineen (1981) noted that dam selection in addition to sire selection improves the response of lambs to vaccination with irradiated *T. colubriformis* larvae compared to sire selection alone. Correlations between records of twin lambs were moderate to high, indicating a net effect of genetic relationship combined with an effect of common environment.

Results from the EBV regression analysis in lambs are shown in Table 3.4. The EBV for MWW and FF were not associated with any of the parasite resistance traits. The EBV for BWT and NB were only associated with MBW. As expected, the MBW was significantly and positively associated with all body weight EBVs and also with MBWT and NB. The IPCV and MPCV increased significantly, and with somewhat similar magnitudes, with increases in EBV for MBWT, WW and PWW. Corresponding to these results, the MFEC and MLFEC decreased with increases in EBV for these traits.

When initial BW was also included in the regression analysis involving EBV for WW, the associations between EBV for WW and MFEC and MLFEC were no longer significant, although the direction of the relationship remained the same (regression coefficients of –851.04 ± 431.2 (ns) and –0.11 ± 0.07 ($P < 0.10$), respectively). The association between EBV for WW and IPCV and MPCV was still significant and positive, although lesser in magnitude (0.97 ± 0.42 ($P < 0.05$) and 1.29 ± 0.42 ($P < 0.01$), respectively). There was no significant relationship between initial BW and MFEC and MLFEC, and there was a positive association between initial BW and IPCV and MPCV (regression coefficient of 0.07 ± 0.02; $P<0.05$ in both cases). Similarly, when initial BW was included in the regression analysis involving EBV for PWW, the association of EBV for PWW was no longer significant for MFEC and MLFEC although the direction of the relationship remained the same (regression coefficients of –188.87 ± 145 and –0.02 ± 0.01, respectively, both ns). The association between EBV for PWW and IPCV and MPCV was also still significant and positive, although lesser in magnitude (0.33 ± 0.13 ($P < 0.05$) and 0.29 ± 0.15 ($P < 0.01$), respectively). Thus, it appears that lambs with improved genetic merit for body weight were clearly not more susceptible to infection and had lower FEC and higher PCV both before and after infection. Also, lambs that were phenotypically larger at the time of infection were able to maintain higher PCV, both initially and when infected. Our results are in agreement with Albers et al. (1987) who reported that there was no significant correlation between resistance to *H. contortus* and productivity in uninfected lambs. Thus, it appears that selection for resistance will not have an unfavorable effect on growth potential of lambs. However, in case of infections with *T. colubriformis*, Morris et al. (2001) and Morris et al. (1997) have reported an unfavourable relationship between resistance and post-weaning gains and yearling fleece weights.

Results from the regression analysis in ewes are shown in Table 3.5. The EBV for MBWT was not associated with any of the parasite resistance traits. As in lambs, MBW was significantly positively associated with all body weight EBVs and NB EBV. Initial PCV was positively associated with EBV for WW, FF and NB and negatively associated with EBV for

MWW. Mean PCV increased with increases in EBV for FF and NB. Unlike in lambs, MFEC and MLFEC appeared to increase with increases in EBV for BWT, WW and PWW. Although not significant (P>0.05), there was a trend for MFEC to be negatively associated with EBV for FF and MLFEC to be positively associated with EBV for NB. Although not significant, there was a trend for MPCV to decrease for increases in all body weight EBVs.

When initial BW was included in the regression analysis involving EBV for WW, the association between EBV for WW and MFEC and MLFEC was still positive and unfavorable (regression coefficients of 356.4 ± 158.4 (P < 0.05) and 0.37 ± 0.18 (P < 0.01), respectively). The association between EBV for WW and IPCV and MPCV was negative and unfavorable (-0.97 ± 0.53 (P < 0.10) and –1.19 ± 0.42 (P < 0.01), respectively). There was no significant association between initial BW and fecal egg count measures and there was a positive association between initial BW and IPCV and MPCV (regression coefficients of 0.15 ± 0.02 and 0.11 ± 0.02 respectively; P<0.01). Similarly, when initial BW was included in the regression analysis involving EBV for PWW, the EBV for PWW was still positively and unfavorably associated with MFEC and MLFEC (regression coefficients of 151.8 ± 50.6 and 0.16 ± 0.06, respectively; both P < 0.01). The EBV for PWW was negatively associated with IPCV and MPCV (-0.37 ± 0.15 and –0.44 ± 0.13, respectively; P<0.01). There was no significant association between initial BW and fecal egg count measures and there was a positive association between initial BW and IPCV and MPCV (regression coefficients of 0.15 ± 0.02 and 0.11 ± 0.02 respectively; P<0.01).

It appears that ewes with a higher genetic merit for growth as lambs are less resistant to infection as adults, with higher FEC after infection, although ewes that are phenotypically heavier at the time of infection were better able to cope with infection as indicated by their higher PCV. Ewes with high genetic merit for growth produce lambs that have higher growth potential and thus are more demanding in terms of nutrients. Bishop and Stear (2001) reported a positive genetic correlation between FEC of ewes in early lactation and the weight of their 4-wk-old lambs. Production of heavier lambs may place extra stress on the ewe during lactation, and the ewe may take more time to recover from the effects of lactation, which render her more susceptible to infection. In this study, fertility and prolificacy do not seem to be associated with parasite resistance, at least in terms of FEC, but were positively associated with IPCV and MPCV. Morris et al. (2001) reported a favourable relationship between resistance to *Trichostrongylus* infections and fertility in terms of number of lambs born per ewe mated. However, ewes with twins have been reported to show a higher PPR than ewes with singles (Courtney et al., 1986; Bishop and Stear, 2001).

Conclusions

Response to *H. contortus* infection is moderately heritable, and selection for increased resistance is possible. Response to infection with *H. contortus* appears to be mediated by different mechanisms in ewes and lambs. Selection for increased resistance will not adversely affect growth in lambs and fertility in ewes.

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Table 3.1 Least square means for mean body weight (MBW, kg)[a], mean fecal egg count (FEC, eggs per gram)[b], mean log-transformed FEC (MLFEC)[b,c], initial packed cell volume (IPCV, %), and mean packed cell volume (MPCV, %)[b] in lambs and ewes.

	Lambs	Ewes
MBW	41.6±0.78	61.1±1.4
MFEC	4298±322	760±183
MLFEC	8.5±0.04	5.1±0.19
IPCV	33.1±0.32	32.2±0.48
MPCV	25.6±0.34	28.0±0.59

[a] Averaged across all measurement times.
[b] Averaged across wk 3 through 7 in lambs and wk 3 through 11 in ewes.
[c] LFEC = ln (FEC + 2000) in lambs and LFEC = ln (FEC + 25) in ewes.

Table 3.2 Genetic parameter estimates for mean body weight (MBW, kg)[a], mean fecal egg count (FEC, eggs per gram)[b], mean log transformed FEC (MLFEC)[b,c], initial packed cell volume (IPCV, %), and mean packed cell volume (MPCV, %)[b] in lambs and ewes.

Item [d]	MBW	IPCV	MPCV	MFEC	MLFEC
Lambs					
σ^2_a	181.76	2.49	4.97	1966058	0.04
σ^2_e	64.75	5.20	3.78	6225626	0.09
σ^2_p	246.51	7.69	8.75	8191684	0.13
H^2	0.74**	0.32**	0.57**	0.24**	0.27**
Ewes					
σ^2_a	74.72	2.11	1.99	195783	0.70
σ^2_{pe}	183.47	1.50	2.41	184906	0.01
σ^2_e	52.78	7.68	3.65	706994	0.57
σ^2_p	310.97	11.29	8.05	1087683	1.28
H^2	0.24†	0.19	0.25*	0.18	0.55**
R	0.83**	0.32**	0.54**	0.35**	0.56**

[a] Averaged across all measurement times.
[b] Averaged across wk 3 through 7 in lambs, and wk 3 through 11 in ewes.
[c] LFEC = ln (FEC + 2000) in lambs and LFEC = ln (FEC + 25) in ewes.
[d] σ^2_a = additive genetic variance; σ^2_{pe} = permanent environmental variance; σ^2_e = error variance; σ^2_p = phenotypic variance; h^2 = heritability; r = between year repeatability.
** P < 0.01; * P < 0.05; † P < 0.10.

Table 3.3 Correlation (from multivariate analysis of variance) between records of lambs and their dams, and between records of twin lambs, for mean body weight (MBW, kg)[a], mean fecal egg count (FEC, eggs per gram)[b], mean log transformed FEC (MLFEC)[b,c], initial packed cell volume (IPCV, %), and mean packed cell volume (MPCV, %)[b].

	Correlation between:	
Measurement	Lamb and dam	Twin lamb
MBW	0.16**	0.50**
IPCV	0.14**	0.27**
MPCV	0.12*	0.29**
MFEC	0.04	0.46**
MLFEC	0.00	0.44**

[a] Averaged across all measurement times.
[b] Averaged across wk 3 through 7 in lambs, and wk 3 through 11 in ewes.
[c] LFEC = ln (FEC + 2000) in lambs and LFEC = ln (FEC + 25) in ewes.
* $P < 0.05$.
** $P < 0.01$.

Table 3.4 Regression coefficients relating parasite resistance traits to estimated breeding values (EBV) for birth weight (BWT, kg), maternal birth weight (MBWT, kg), weaning weight (WW, kg), maternal weaning weight (MWW, kg), fall fertility (FF, %), number born (NB, %), and post-weaning weight (PWW, kg) in lambs.

EBV	Parasite resistance trait [a]				
for:	MBW	IPCV	MPCV	MFEC	MLFEC
BWT	15.48±4.10 **	2.02±1.74	-2.97±1.83	2728±1815	0.34±0.24
MBWT	4.36±2.15*	2.64±0.92*	2.44±0.97*	-2809±955**	-0.31±0.13*
WW	9.36±0.69**	1.45±0.35**	1.67±0.37**	-953±370*	-0.13±0.04**
MWW	0.93±0.79	0.31±0.42	0.13±0.42	-92±427	-0.02±0.04
FF	0.05±0.05	0.01±0.02	0.03±0.02	-3±23	-0.00±0.00
NB	0.18±0.08*	0.05±0.03	-0.03±0.03	39±34	0.00±0.00
PWW	3.24±0.23**	0.51±0.11*	0.46±0.13*	-304±121*	-0.04±0.02*

* $P < 0.05$.

** $P < 0.01$.

[a] MBW = Mean body weight during the period of the study; IPCV = Initial PCV at the time of challenge; MPCV = Mean PCV (avg. of wk 3 to 7 post-infection); MFEC = Mean FEC (avg. of wk 3 to 7 post-infection); MLFEC = Mean log-transformed (FEC+2000) (avg. of wk 3 to 7 post-infection).

Table 3.5 Regression coefficients relating parasite resistance traits to estimated breeding values (EBV) for birth weight (BWT, kg), maternal birth weight (MBWT, kg), weaning weight (WW, kg), maternal weaning weight (MWW, kg), fall fertility (FF, %), number born (NB, %), and post weaning weight (PWW, kg) in ewes.

EBV	Parasite resistance trait [a]				
for:	MBW	IPCV	MPCV	MFEC	MLFEC
BWT	22.77±6.12**	2.27±2.66	-3.85±2.20†	1549±821†	2.27±0.86*
MBWT	-0.41±2.23	-1.34±0.97	-0.37±0.81	-295±299	-0.09±0.31
WW	9.69±1.07**	1.01±0.51*	-0.04±0.42	361±161*	0.42±0.18*
MWW	-1.09±0.77	-1.21±0.37**	-0.57±0.31†	9±114	-0.09±0.13
FF	0.08±0.06	0.05±0.03*	0.05±0.02*	-15±8†	-0.01±0.01
NB	0.30±0.08**	0.10±0.04**	0.06±0.03*	11±11	0.02±0.01†
PWW	2.79±0.31**	0.11±0.15	-0.13±0.13	145±46**	0.15±0.04**

* $P < 0.05$.

** $P < 0.01$.

† $P < 0.1$.

[a] MBW = Mean body weight during the period of the study; IPCV = Initial PCV at the time of challenge; MPCV = Mean PCV (avg. of wk 3 to 11 post-infection); MFEC = Mean FEC (avg. of wk 3 to 11 post-infection); MLFEC = Mean log-transformed (FEC+25) (avg. of wk 3 to 11 post-infection).

CHAPTER 4

Between-breed variation in resistance to *Haemonchus contortus* infection in sheep

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ABSTRACT: The objective of this study was to evaluate breed differences in resistance to *Haemonchus contortus* in sheep. A total of 181 ewe lambs representing crossbred Dorset (**DO**) and Dorper (**DP**) (out of 1/2 –Dorset, 1/4 –Rambouillet, 1/4-Finnsheep ewes) and straightbred Katahdins (**KT**) were evaluated over 3 yr. An additional 144 DO, DP, KT and Barbados Blackbelly x St. Croix (**HH**) wethers were evaluated over 2 yr. Lambs were weaned at 60 to 90 d of age. After deworming at about 4 mo of age, ewe lambs received a standard dose of infective larvae and were evaluated in drylot whereas wethers were evaluated on pasture under conditions of natural infection. Each sex was analyzed separately. Initial analysis was performed by a repeated-measures analysis of variance of egg counts per gram of feces (**FEC;** epg), log transformed FEC (**LFEC**), packed cell volumes (**PCV**; %), and body weights (**BW**; kg) collected at 3, 4, 5 and 6 wk after deworming and reinfection. The model included year, breed, week (the repeated effect), and all interactions. Breed influenced all traits ($P<0.05$) except BW in ewe lambs and PCV in wethers. Year and week influenced ($P<0.05$) all traits. At most times, DP had higher FEC, DO had lower PCV, and KT and HH had lower FEC and higher PCV. Summary traits were defined as initial PCV (IPCV), and mean values for BW (MBW), FEC (MFEC), LFEC (MLFEC), and PCV (MPCV) over 4 post-infection measurements. These traits were analyzed using a multivariate analysis of variance using a model including year, breed, and year x breed interaction. The DP were clearly not more resistant to parasites than DO but were able to cope better by maintaining higher PCV and similar BW compared to DO. The KT and HH were more resistant with lower FEC. Breed differences were more apparent when infection levels were higher, and DO and DP performed better when infection levels were low and all animals were on a better plane of nutrition. Important breed differences in resistance to *H. contortus* in sheep thus appear to exist.

Introduction

Endoparasitic infections are a major constraint for sheep producers all over the world. They lead to increases in costs of management and treatment, loss of production, and in severe cases, even mortality. *Haemonchus contortus* is prevalent in tropical and subtropical parts of the world and is also important in the temperate regions, especially during warm and wet conditions of spring and summer. Infection with *H. contortus* is probably one of the more devastating endoparasitic infections; the worm sucks blood, which may lead to anemia and death, and it is a very prolific parasite. There have been increasing reports from many parts of the world regarding development of anthelminthic resistance in several parasite species (Overend et al., 1994; Gopal et al., 1999; van Wyk et al., 1999). Also, with growing concern regarding use of chemicals in animal production, the focus in recent years has been to reduce dependency on anthelminthics to control the disease.

One option is to breed and raise sheep that are resistant to these parasites. Over the past several decades, many studies have indicated that variation exists in response to parasitic infection, including *Haemonchus*, both within (Bishop et al., 1996; Woolaston and Windon, 2001; Morris et al., 1997) and among different breeds of sheep. Most studies involving breed differences have used tropical and subtropical breeds of sheep such as the Red Maasai (Wanyangu et al., 1997; Baker et al., 1999), St. Croix, Florida Native (Zajac et al., 1990; Gamble and Zajac, 1992), and Barbados Blackbelly (Yazwinski et al., 1981), which have been reported to be more resistant to trichostrongyle infections compared to temperate breeds like Dorset (DO) and Rambouillet.

The Katahdin (KT) is a hardy hair-type sheep developed in the United States from African hair type sheep and wooly British sheep. Dorpers (DP) are sheep of South African origin that were originally developed from Dorset Horn and Blackheaded Persian sheep breeds to meet the challenges of producing good quality meat in arid regions both under extensive and intensive management systems. Both breeds have good production capabilities, do not require shearing, and are relatively parasite resistant, although Baker et al. (1999) reported that Dorpers are more susceptible to parasitism than the Red Maasai of Africa. The objective of this study was to evaluate breed differences among crossbred DO, crossbred DP, straightbred KT, and Caribbean hair sheep crosses (HH; St. Croix x Barbados Blackbelly) in response to either a standard artificial *H. contortus* challenge or a natural pasture challenge.

Materials and Methods

The experiment was conducted in two parts over a period of 3 yr. The first part involved artificial challenge of DO, DP and KT ewe lambs, and the second part involved natural pasture challenge of DO, DP, KT, and HH wethers.

Animals and experimental design. The DO and DP lambs were produced at the Southwest Virginia Agricultural Research and Extension Center, Glade Spring, VA, by mating Dorset and Dorper rams to ewes of 50% Dorset, 25% Rambouillet and 25% Finnsheep breeding. In 2000, DP lambs were sired by four imported rams used by AI. In 2001 and 2002, two different DP sires were used in each year by natural service. The four rams used in 2001 and 2002 were obtained from two different flocks and were offspring of four different sires. Thus a total of eight DP rams by eight different sires were represented. Three DO rams were used in each year. One ram was used for 2 yr; all other rams were used for only 1 yr. Seven of the eight rams were produced in the Virginia Tech Dorset flock and represented five different sires. The eighth ram was purchased from another flock and was the ram that was used for 2 yr.

Unregistered, commercial KT ewe lambs were purchased from private breeders. Most were born in April, although six were born between March 20 and April 1. In each year, ewe lambs were purchased from four different flocks (two to six lambs per flock). Three flocks were sampled in each of two years, so the total number of flocks sampled was ten, with two to 11 ewe lambs per flock. In most, but not all cases, two sires were represented for each flock, to give a total number of approximately 15 KT sires.

The KT wether lambs were purchased in 2001 and 2002. The 2001 lambs (n = 15) came from a single flock and represented two sires. The 2002 lambs came from four flocks (including a second sample of wethers from the flock sampled in 2001), with three to five wethers per flock.

The HH wethers were produced at the Virginia Tech Sheep Center in Blacksburg. Lambs were produced by reciprocal crossing of St. Croix and Barbados Blackbelly ewes and rams. A few backcrosses were represented in the 2002 lambs and were produced by mating Barbados Blackbelly or St. Croix rams to F_1 St. Croix x Barbados Blackbelly ewes. Numbers of sheep of each breed group utilized in each year are given in Table 4.1.

Ewe lambs were evaluated in 2000, 2001 and 2002. Wether lambs were evaluated only in 2001 and 2002. The DO and DP crossbred ewe lambs were weaned at about 60 d of age in 2000 and 2001, moved to a drylot, and fed a diet consisting of approximately 14.5 % CP, 2.5 % fat, and 23 % fiber, with 71 % TDN. In 2002, ewe lambs were weaned at about 90 d after being creep fed for 1 mo before weaning, as they were smaller than in previous years and had a bad footrot problem. All KT lambs were weaned and delivered to Glade Spring at approximately 60 d of age. Dorper, DO and KT ewe lambs were maintained together on drylot from the time of weaning until the end of the study. Katahdin and HH wether lambs were also weaned and transferred to Glade Spring at about 60 d of age. Purchased wether lambs were maintained in drylot until the DO and DP wether lambs were weaned at about 60 to 90 d of age; after that time all wether lambs were maintained as contemporaries on pasture. In 2001, wether lambs were creep fed after weaning at a level designed to maintain daily gains of at least 0.2 kg/d, and in 2002 they were fed ad libitum.

At 4 to 5 mo of age, all lambs were dewormed with levamisole hydrochloride (Tramisol; Schering-Plough Animal Health, NJ) at the label recommended dose rate. Ewe lambs were then dosed with approximately 10,000 infective *H. contortus* larvae 2 d after deworming in 2000 and 2001 and 4 d after deworming in 2002 and subsequently remained in drylot. The larval culture was obtained from USDA Agricultural Research Service in Beltsville, MD. Wether lambs were returned to infected pastures after deworming and were evaluated on pasture under conditions of natural infection. Jugular blood samples to estimate packed cell volume (PCV, %), rectal fecal samples to estimate fecal egg count (FEC, eggs/gm), and body weight (BW, lbs) measurements were obtained at 3, 4, 5 and 6 wk after infection (for ewe lambs) or deworming and return to infected pastures (for wethers). In 2001 and 2002, initial values for PCV and BW were also obtained at the time of infection (in ewe lambs) or deworming (in wethers). Initial BW (IBW) and PCV were not measured in 2000. Body weight 10 d post-infection was used as the initial weight in 2000; it was assumed to be unlikely that body weight at this time would have been affected by parasitism. In case of ewe lambs, BW measures were available only at 4 and 6 wk post infection in 2000, hence for BW analysis only weights taken at 4 and 6 wk post infection were considered in all years.

Animals were removed from the experiment and dewormed if their PCV fell below 18% and they lost weight. In 2001, 14 wethers (five DO, six DP, two KT, and one HH) with low PCV were dewormed after 5 wk post-infection, one DP wether lamb died at 4 wk post-infection due to causes apparently unrelated to parasitism, and nine ewe lambs (five DO and four DP) were accidentally dewormed after sampling at 5 wk post-infection and were removed from the experiment. In 2002, one ewe lamb was removed from the study and dewormed after sampling

at 5 wk post-infection because of low PCV and two wether lambs (one KT and one DP) died after 4 wk post-infection from causes apparently unrelated to parasitism. All lambs were dewormed immediately after final sampling.

Experimental samples. Fecal egg counts were estimated using the Modified McMaster's method (Whitlock, 1948) with each egg counted representing 25 eggs/gm (epg). Samples of less than 2 gm were discarded. When no eggs were observed on the slide, FEC was recorded as zero. Blood was collected from the jugular vein into Vacutainer tubes coated with EDTA, and PCVs were estimated the same day using the microhaematocrit centrifuge method. Missing observations occasionally resulted when fecal samples of adequate size could not be obtained or from clotting of blood samples. The frequency of missing values was 11 % for FEC and 6 % for PCV in wethers and 10.5 % for FEC and 3.6 % for PCV in ewe lambs.

Statistical analysis. Data were initially analyzed by analysis of variance using the general linear models procedure of the SAS software package (SAS Instt. Inc., Cary, NC). Data from ewe lambs and wethers were analyzed separately. Preliminary analysis indicated that the distribution of FEC was not normal; observed values were thus transformed as LFEC = ln(FEC + 100). One very high FEC observation of 30,725 eggs/gm for a 2002 DP ewe lamb was deleted as an outlier. For each sex, a repeated-measures analysis of variance (using PROC MIXED in SAS) was used to describe patterns of change in weekly measures of BW, FEC, LFEC and PCV. The model included fixed effects of year, breed, week (the repeated effect) and all interactions.

A set of summary traits was also defined and used to investigate interrelationships among measured variables. These summary traits included initial PCV (IPCV) and mean values for BW (MBW; in ewe lambs this was the mean of measurements taken at wk 4 and wk 6 post-infection), PCV (MPCV), FEC (MFEC) and LFEC (MLFEC) over the four post-infection times. In calculation of summary traits, missing values for FEC or PCV were replaced by predicted values derived from a nested analysis of variance (using PROC GLM of SAS) including fixed effects of year, breed, week, their two-way interactions and a random effect of animal nested within breed and year. Use of this model to predict missing values was required because the repeated-measures analysis (using PROC MIXED in SAS) does not provide for prediction of missing values. The summary traits were then analyzed using multivariate analysis of variance with year, breed, their two-way interaction, and the continuous effect of IBW (expressed as a deviation from the breed-year mean IBW) in the model. For ewe lambs, values for IPCV were not available for 2000. Correlations among summary traits were obtained from these analyses. In 2002, one KT ewe lamb had very low FEC at most measurement times (=25 epg) and four KT ewe lambs had very high FEC and low PCV. These five KT were removed from the dataset and the analysis was rerun to see if it produced significantly different results. Supplemental regression analyses were also performed to quantify associations between MPCV and IPCV, MFEC and MPCV, MLFEC and MPCV, MFEC and MBW, and MLFEC and MBW.

Results

Ewe lambs. For the repeated-measures analysis, the three-way interaction did not have an effect on any of the traits. Effects of year, week, and year x week interaction were significant ($P<0.05$) for all traits. There was an effect of breed ($P<0.05$) on all traits except BW ($P = 0.29$).

Breed x wk interaction was significant (P<0.05) only for FEC and LFEC and year x breed interaction was significant (P<0.05) only for BW and PCV. Changes in BW, PCV, and back transformed LFEC for ewe lambs over time for each year are depicted in Fig 4.1 through 4.3. Ewe lambs generally did not lose weight during the study period, except for DP ewe lambs in 2001, which lost some weight in the last week. The FEC generally increased till the 5th wk post-infection and then began to decline. However exceptions to this general pattern were seen in KT in 2000 and DO in 2002, which showed a continual increase in FEC throughout the measurement period. Also, 2001 DO showed an early decline in FEC starting at the 4th wk post-infection. The PCV declined initially until wk 4, wk 3, and wk 5 post-infection, respectively, in 2000, 2001 and 2002, and then increased gradually or remained relatively stable.

Year and breed effects were significant (P<0.01) for all summary traits, and year x breed interaction was significant for MBW and MPCV (P<0.05). Year x breed least square means for IBW, IPCV, MBW, MFEC, back transformed MLFEC, and MPCV are shown in Fig 4.4.

All years differed in IBW (P<0.05) of the lambs; lambs were heaviest in 2000 and weighed the least in 2001. Mean BW was higher in 2000 than in 2001 and 2002 (P<0.05). In 2000, DP were much heavier (P<0.05) than DO and KT in terms of both IBW and MBW. In 2001, DP ewe lambs were not significantly different than DO or KT for IBW and were lighter (P<0.05) than both DO and KT in terms of MBW. In 2002, DP were heavier (P<0.05) than KT and were not different from DO for IBW and MBW.

Initial PCV was higher (P<0.05) in 2002 compared to 2001, and MPCV was higher (P<0.05) in 2000 than in 2001 and 2002. The KT generally had higher IPCV than DO (P < 0.05) and a higher (P<0.05) MPCV than both DP and DO. There were no differences between DO and DP for IPCV and MPCV. Although, overall, KT had a higher IPCV than DO, there were no significant differences between breeds for IPCV within each year. In 2000, KT had higher MPCV than DO but had similar MPCV as DP. In 2001, KT had a higher MPCV than both DO and DP. In 2002, there were no significant differences between breeds for MPCV.

Both MFEC and MLFEC were lower (P<0.05) in 2000 compared to 2001 and 2002. The DP generally had highest MFEC and MLFEC, and KT had similar MFEC but similar or lower MLFEC than DO; overall, DP had higher (P<0.05) MFEC than DO and KT and all breeds differed (P<0.05) in MLFEC. In 2000, there were no differences between breeds for MFEC and MLFEC. In 2001 and 2002, DP had highest MFEC and MLFEC and there were no differences between DO and KT in terms of MFEC. Although the log transformation did not affect breed differences in 2002, KT had lowest MLFEC in 2001, such that all breeds were different in terms of MLFEC in 2001.

Four KT in 2002 had exceptionally high FEC and low PCV and one KT did not show any effects of parasitism with very low FEC across all measurement periods (FEC = 25 epg). When these 5 KT were removed from the data set and the analysis performed again, certain differences in results were seen. Results pertaining to IBW, MBW, and IPCV did not change significantly. However, MFEC for KT in 2002 declined from 3574 epg to 2152 epg and back transformed MLFEC for KT in 2002 declined from 1720 epg to 1326 epg so that in 2002 all breeds were different from each other in terms of MFEC and MLFEC and the year-breed interaction for

MFEC was now significant (P<0.05). Also, MPCV for KT in 2002 increased from 26.12 % to 26.93 % and the year-breed interaction for MPCV was no longer significant. The KT were more variable in response to infection, with a coefficient of variation for LFEC over the 3 yr ranging from 15 to 19 % compared with 7 % to 12 % for DO and 6 % to 13 % for DP.

Correlations between MBW, MPCV, MFEC and MLFEC after adjustment for year by breed IBW are given in Table 4.2. Both FEC measures were negatively correlated with MBW and MPCV, and highly positively correlated with each other. Mean PCV and MBW were not correlated. Initial PCV was not correlated to any of the other summary traits and is not shown in the table. Initial BW did not have an effect on any of the summary traits except MBW (P<0.01); each 1 kg increase in IBW was associated with an increase of 0.98 ± 0.04 kg in MBW.

Regression of MPCV on IPCV did not reveal any associations between the two traits. Regression of MPCV on both measures of FEC indicated that animals with higher FEC have lower MPCV; an increase in MFEC of 100 eggs/gm led to a 0.07 ± 0.01 % decrease (P<0.05) in MPCV and one unit increase in MLFEC led to a 1.85 ± 0.26 % decrease (P<0.05) in MPCV. After adjustment of MPCV for MFEC, DP had a higher (P<0.05) MPCV than DO and were similar in MPCV to KT. Regression of MBW on MFEC and MLFEC indicated that increasing FEC measures adversely affected (P<0.05) MBW; one unit increase in MLFEC led to a 1.65 ± 0.65 kg decrease (P<0.05) in MBW, and an increase of 1,000 epg of MFEC led to an decrease of 0.51 ± 0.23 kg (P<0.05) in MBW. After adjustment of MBW for MFEC or MLFEC, DO were similar to both DP and KT in FEC measures.

Wethers. For the repeat measures analysis, the three-way interaction was significant for FEC and LFEC (P<0.05). Year x breed interaction was significant for BW and PCV. Effects of breed and breed x week interaction were significant (P<0.05) for all traits except PCV. Effects of year, week and year x week interaction were significant (P<0.05) for all traits. Changes in BW, PCV and back transformed LFEC for wethers over time for each year are depicted in Fig 4.5 and 4.6. Overall, wethers did not lose weight over the study period. The HH lost weight initially in 2001 but then recovered by 4th week post-infection. The FEC continued to increase until the last measurement time in 2001, but in 2002 they started to decline after 5th week post-infection. The PCV increased from the time of deworming until 3rd week post-infection, except for KT and HH in 2002, which appeared to decline, although not significant. Thereafter, PCV continued to decline until the end in 2001, but remained relatively stable in 2002. Generally, HH had lowest BW and FEC at all measurement times. The DO and DP had higher FEC than KT and HH. The DO and DP had lower PCV than HH and KT in 2001 and had higher PCV than HH and KT in 2002 at most post-infection times.

Year had a significant effect (P<0.05) on all summary traits and breed had a significant effect (P<0.05) on all summary traits except MPCV. Year x breed interaction was significant (P<0.05) for IPCV, MPCV and MBW. Year x breed least square means for IBW, MBW, IPCV, MPCV, MFEC and back transformed MLFEC are shown in Fig 4.7. Initial body weight, MBW, IPCV and MPCV were higher (P<0.05) and MFEC and MLFEC were lower (P<0.05) in 2002 than in 2001.

Overall, DO, DP, and KT had higher IBW than HH, and DO and DP were heavier than HH, and the KT were intermediate in terms of MBW ($P<0.05$). In 2001, DO and DP were heavier ($P<0.05$) than KT and HH in terms of IBW and MBW. However, in 2002, KT had similar IBW to DO and DP and were heavier ($P<0.05$) than all others in terms of MBW.

There were no clear cut differences between breeds in terms of IPCV and MPCV, although overall for the two yr, DO had the lowest ($P<0.05$) IPCV and DP had the highest ($P<0.05$) MPCV. In 2001, DO had the lowest IPCV, KT and HH had the highest IPCV, and DP were intermediate ($P<0.05$). However, the differences between breeds for MPCV were minimal; the only difference was that HH had a higher ($P<0.05$) MPCV than DO. In 2002, although there were no significant differences between breeds for IPCV, DP had higher ($P<0.05$) MPCV compared to HH and KT.

Overall, both MFEC and MLFEC were highest in DO and DP, lowest in HH, and the KT were intermediate ($P<0.05$). However, in 2001, HH had lowest ($P<0.05$) MFEC and there were no significant differences between DO, DP and KT. In 2002, DO and DP had higher ($P<0.05$) MFEC and MLFEC than KT and HH.

Correlations between all summary traits after adjustment for year-breed IBW are given in Table 4.2. Both FEC measures were negatively correlated with MBW, MPCV and IPCV, and highly positively correlated with each other. Mean PCV ($P < 0.01$) and IPCV ($P < 0.1$) were positively correlated with MBW and moderately positively correlated with each other. Initial BW was positively associated with MBW, IPCV and MPCV and negatively associated with MFEC and MLFEC.

Regression of MPCV on IPCV indicated a favorable association between them; MPCV increased by 0.28 ± 0.04 % for each unit increase in IPCV ($P<0.05$). Regression of MPCV on both measures of FEC indicated that animals with higher FEC have lower MPCV; an increase in MFEC of 1,000 epg led to a decrease of 1.7 ± 0.3 % in MPCV and one unit increase in MLFEC led to 2.6 ± 0.48 % decrease ($P<0.05$) in MPCV. Adjustment of MPCV for MFEC did not affect breed differences but after adjustment of MPCV for MLFEC, DO were significantly higher than HH or KT ($P<0.05$). Regression of MBW on MFEC and MLFEC indicated that FEC measures were unfavorably associated with MBW ($P<0.05$); an increase of 1,000 epg of MFEC led to a decrease of 1.57 ± 0.46 kg ($P<0.05$) in MBW and one unit increase in MLFEC led to 2.86 ± 0.79 kg decrease ($P<0.05$) in MBW.

Discussion

Ewe lambs. Ewe lambs generally did not lose weight during infection. The patterns of increase in FEC over time correspond closely with the changes in PCV; PCV declined as FEC increased, and began to increase when FEC started to decline. The PCV levels corresponded with FEC levels in all years; years with high FEC had low PCV and vice versa. The FEC declined and PCV stabilized by the end of the study period in the case of artificial infection without re-infection.

The DP were generally heavier than KT and had similar or higher weight than DO. DO and KT had similar body weights. In 2000, DP lambs were much heavier than DO or KT. This was because of use of good AI DP rams in 2000, which produced heavier lambs. In 2001, DP weighed less than DO and KT. This may have been because the DP in 2001 were generally unthrifty and slightly younger than other lambs and also were more heavily parasitized as evidenced by their FEC.

Mean BW and MPCV were higher and MFEC and MLFEC lower in 2000 compared to 2001 and 2002. This was probably because the 2000 ewe lambs were relatively healthy and generally bigger at the start of the experiment, notwithstanding the fact that the IBW on these animals is actually BW taken 10 d post-infection. It also appears that FEC need to be high enough for breed differences to be expressed. There were no breed differences in MFEC in 2000 when infection levels were lower but they were more appreciable in 2001 and 2002 when infection levels were higher.

Ewe lambs in 2002 had an advantage over those in 2001 in terms of IBW and IPCV, which may have been because of the fact that they were weaned later and also were fed better before infection. However, their MBW, MPCV and MFEC were similar in the two years.

Generally, DP had highest FEC at almost all times in all years, KT had the lowest FEC and highest PCV at all times, and DO had lowest PCV at almost all times except in 2002, although these differences were not always significant. Also, DP showed the steepest increases in FEC after infection. Although differences between breeds were not strong for IPCV, KT had higher MPCV than both DO and DP. Although DP had higher FEC than DO, they had similar IPCV and MPCV levels as the DO. Thus, DP do not appear to be resistant in terms of FEC but they do show an advantage in terms of a better PCV. Indeed, after adjustment of MPCV for MFEC, DP were ranked higher than DO and were similar to KT. Therefore, under conditions of artificial challenge with no re-infection, KT are resistant, with low FEC and high PCV. Although DP have lower resistance compared to DO as evidenced by their FEC, DP appear to cope with infection better by maintaining similar BW and higher PCV compared to DO.

Wethers. Wethers did not lose weight over the period of the study. Wethers showed an initial increase in PCV after deworming as they recovered from effects of previous infection acquired on pasture. This result is in contrast to that observed in ewe lambs, which showed an initial decline in PCV after deworming and infection. The FEC in wethers are expected to increase through out the period of study as they were being continually re-infected. This pattern was seen in 2001. However, in 2002, FEC started to decline by the 5th week post-infection and PCV remained stable through out the period. Although it is also possible that levels of infection on pasture were lower in 2002, it is more likely that this result occurred because the lambs were being fed better and so did not show the effects of parasitism. Preston and Allonby (1978) and Kambara et al. (1993) have reported that animals on a better plane of nutrition and especially protein supplementation appear to be more resistant. The FEC were much lower in wethers compared to ewe lambs. It may be because they were facing a natural challenge that might have been much lower than the artificial challenge level, and also, the strain of parasite in the larval culture might be of a more fecund species compared to the strain on the pasture.

Estimates for MFEC and MLFEC may have been underestimated and estimates for MPCV overestimated for DO and DP in 2002 because of the five DO and six DP that were removed from the study at 5th week post-infection. If they had been continued on the study, these breeds may have been estimated to have much higher FEC and much lower PCV than that predicted.

The DP and DO had higher FEC compared to HH, and KT tended to be intermediate in both years; correspondingly, at least in 2001, the PCV after infection were highest in HH and lowest in DO and DP, and intermediate in KT. However, when infection levels were low and wethers were better fed, as in 2002, DO and DP wethers had higher PCV compared to HH and KT, although IPCV were not different amongst breeds and FEC were higher in DO and DP. Like in ewe lambs, DP wethers generally tended to have higher FEC compared to DO but also maintained higher PCV under infection.

IPCV was correlated with other summary traits in wethers but not in ewe lambs. IPCV in wethers is influenced by existing infection levels on the pasture and is thus similar to PCV under infection, unlike in ewe lambs.

Breed differences, especially between DO and DP, were not as evident in wethers as in ewe lambs. It is unlikely that this was because of differences in sex. It is more likely that this was because of the relatively low infection levels in wethers wherein breed differences do not become apparent, like in the case of ewe lambs in 2000. In cases of both artificial infection and a natural pasture challenge, differences regarding FEC were clear. The DP had high FEC, although under low infection levels, DO and DP had similar FEC, and KT and HH had low FEC. Differences between breeds for PCV were not clear-cut. However, it appears that DO have the lowest PCV levels. When the plane of nutrition is high, or infection level is low, differences between breeds regarding PCV are not apparent.

In Africa, Dorper ewes (Baker et al., 1999) and lambs (Mugambi et al., 1997) have been reported to be relatively susceptible to *H. contortus* infections, with low PCV and higher FEC than the Red Maasai in case of both natural and artificial challenge. However, Red Maasai x Dorper ewes were as susceptible as the Dorpers. The higher PCV seen in DP in our study may be because of better feeding conditions compared to the African studies. Dorset lambs have been reported to be more susceptible to *H. contortus* infection compared to St. Croix (Gamble and Zajac, 1992) and Barbados Blackbelly x Dorset lambs (Yazwinski et al., 1981). Gamble and Zajac (1992) reported that under conditions of natural infection, significant breed differences were observed starting 47 d after first exposure at 8 wk of age, and then again at 24 d after deworming and re-infection. They reported that St. Croix lambs had 99% fewer worms in the abomasum compared to Dorset lambs, and that St. Croix were more refractory to re-infection and had higher levels of acquired resistance in response to both natural and experimental infections with *H. contortus*. Zajac et al. (1990) found that 9- to 10-month-old Dorset x Rambouillet lambs were less resistant to infection with *H. contortus* than age matched St. Croix and Florida Native lambs. Courtney et al. (1985) have also reported that at 4 to 6 months of age, in case of secondary infection with *H. contortus*, St. Croix lambs were more resistant than domestic crossbred lambs (½ - Suffolk, ¼ - Dorset, ¼ - Finnsheep or ½ - Dorset, ¼- Finnsheep, and ¼- Rambouillet). However, Todd et al. (1978) did not find any breed differences in response to an

artificial *H. contortus* infection when comparing Barbados Blackbelly x Targhee and straightbred Targhee lambs that were raised worm-free and then infected with different doses (10,000 and 25,000) of larvae at 4 mo of age, although lambs receiving a heavier dose had much higher FEC and worm burdens, and lower PCV post-infection. This suggests that lambs need sufficient exposure to parasites before their immune system reacts to the infection fully and breed differences become evident. Also, Courtney et al. (1985) reported that variations among breeds were not consistent in response to a primary infection in lambs of 4 to 6 mo or age.

Conclusions

Breed differences exist in response to both artificial infection and natural pasture challenge with *H. contortus*. Hair sheep and Katahdin are relatively resistant to infection and have lower FEC. Dorpers are not resistant and have higher FEC, but they appear to cope better compared to Dorsets as evidenced by higher PCV and similar BW compared to Dorsets. Dorset and Dorper are better able to cope with infections compared to KT and HH when all are on a better plane of nutrition. Breed differences are not very apparent, especially between Dorset and Dorper, when infection levels are low.

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Table 4.1 Numbers of ewe (E) and wether (W) lambs of each breed group evaluated in each year of the study.

	2000	2001		2002	
Breed group [a]	E	E	W	E	W
DO	23	37	27	12	15
DP	10	24	25	20	19
KT	20	17	15	18	15
HH	-	-	15	-	13

[a] Dorper (DP) and Dorset (DO) crosses were produced by mating Dorper and Dorset rams to 25% Finnsheep, 50% Dorset and 25 % Rambouillet ewes; Katahdin (KT) lambs were purchased at weaning; and hair sheep lambs (HH) are crosses between St. Croix and Barbados Blackbelly.

Table 4.2 Residual correlations between mean body weight (MBW), mean packed cell volume (MPCV), mean fecal egg count (MFEC), mean log fecal egg count (MLFEC) and initial packed cell volume (IPCV) in ewe lambs [a] (below the diagonal) and wethers (above the diagonal).

	MBW	MPCV	MFEC	MLFEC	IPCV
MBW		0.19 **	-0.25 **	-0.25**	0.15 †
MPCV	0.14		-0.46 **	-0.39 **	0.32 **
MFEC	-0.24 **	-0.47 **		0.82 **	-0.28 **
MLFEC	-0.16 **	-0.46 **	0.80 **		-0.28 **

[a] Correlations involving IPCV in ewe lambs not available from this analysis as IPCV was analyzed separately.

** $P < 0.01$.

† $P < 0.1$.

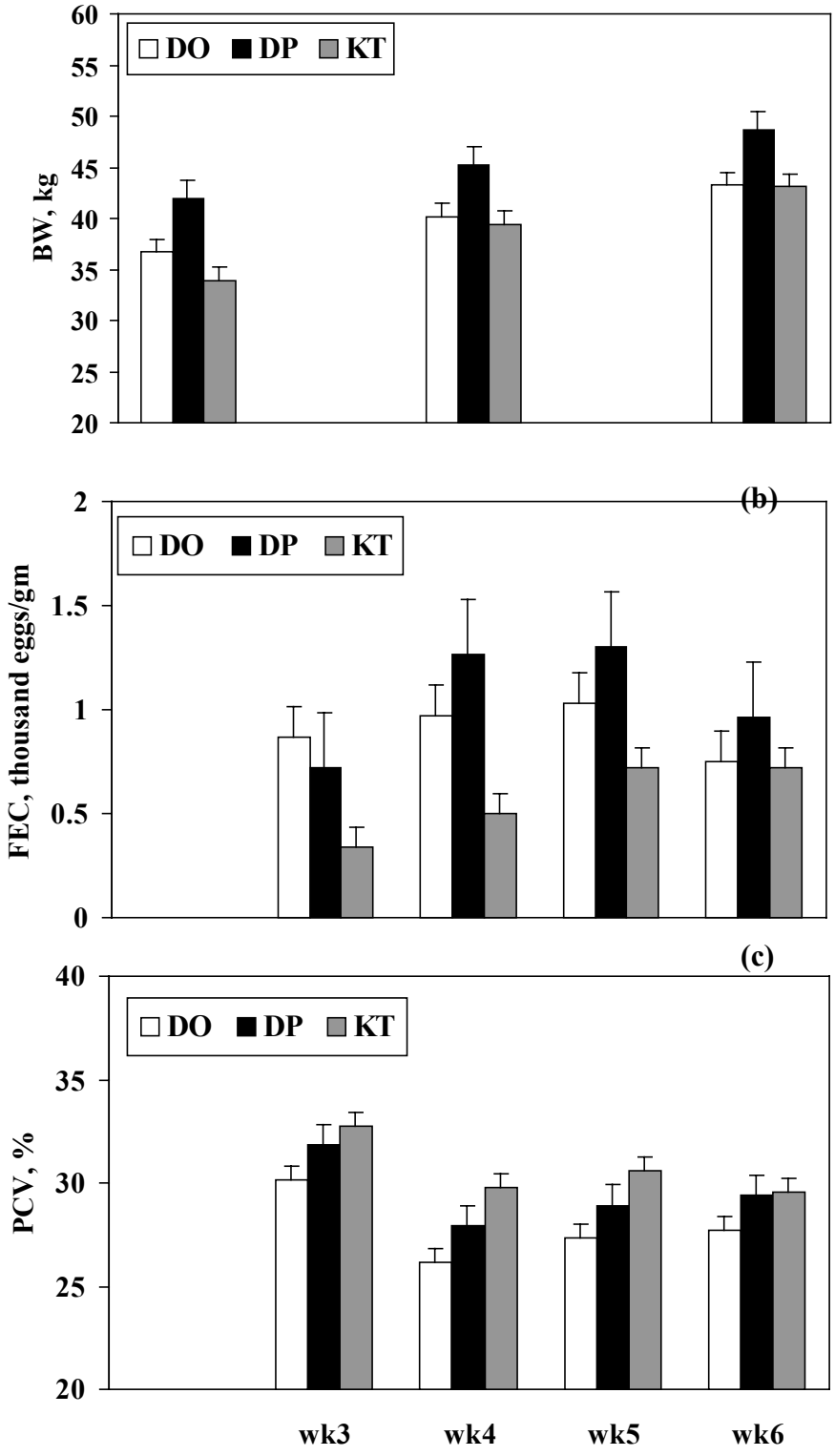

Fig 4.1 Breed x week least square means for: (a) body weight (BW), kg, (b) back transformed log fecal egg count (FEC), eggs/gm, and (c) packed cell volume (PCV), %, in 2000 Dorset (DO), Dorper (DP), and Katahdin (KT) ewe lambs.

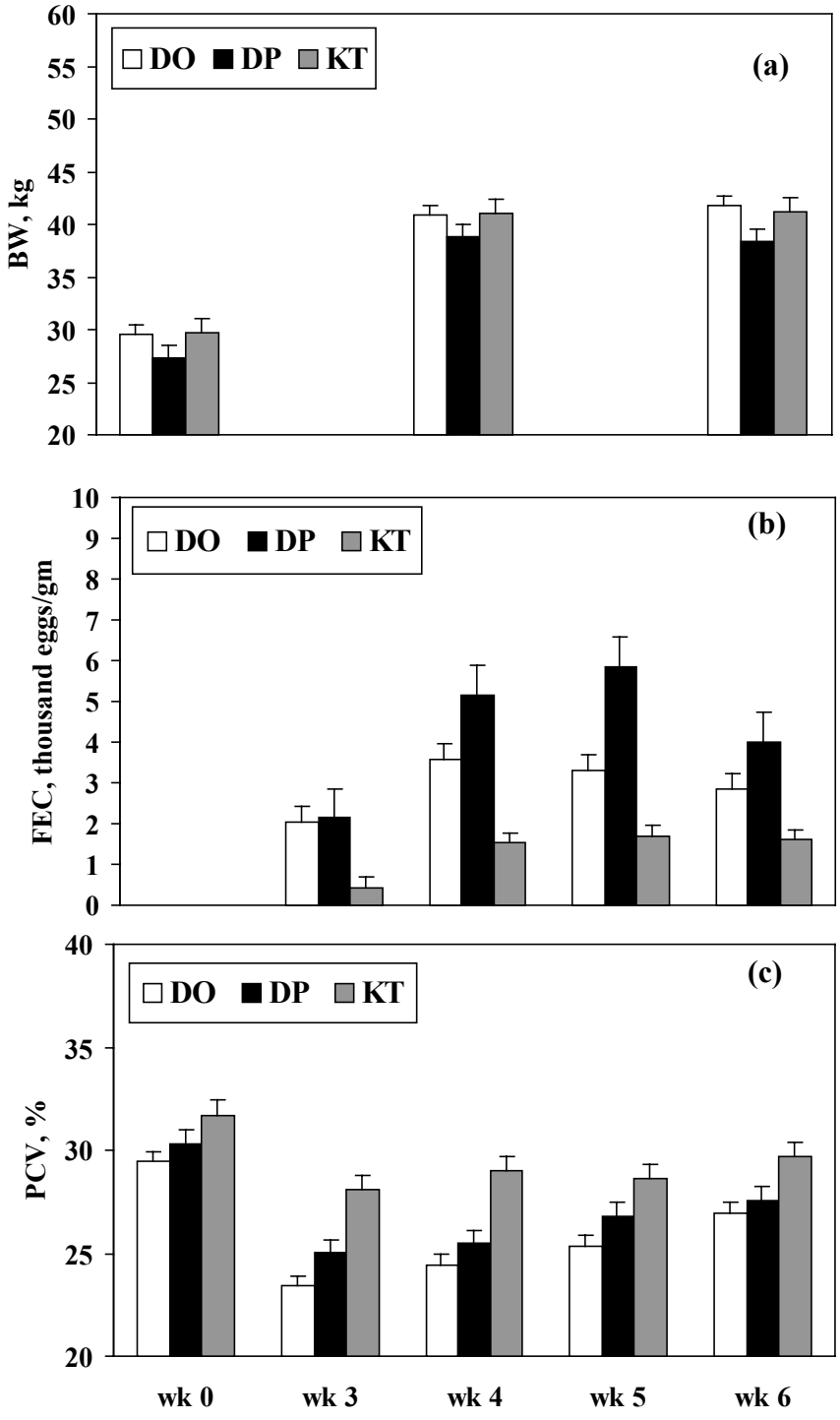

Fig 4.2 Breed x week least square means for: (a) body weight (BW), kg, (b) back transformed log fecal egg count (FEC), eggs/gm, and (c) packed cell volume (PCV), %, in 2001 Dorset (DO), Dorper (DP), and Katahdin (KT) ewe lambs.

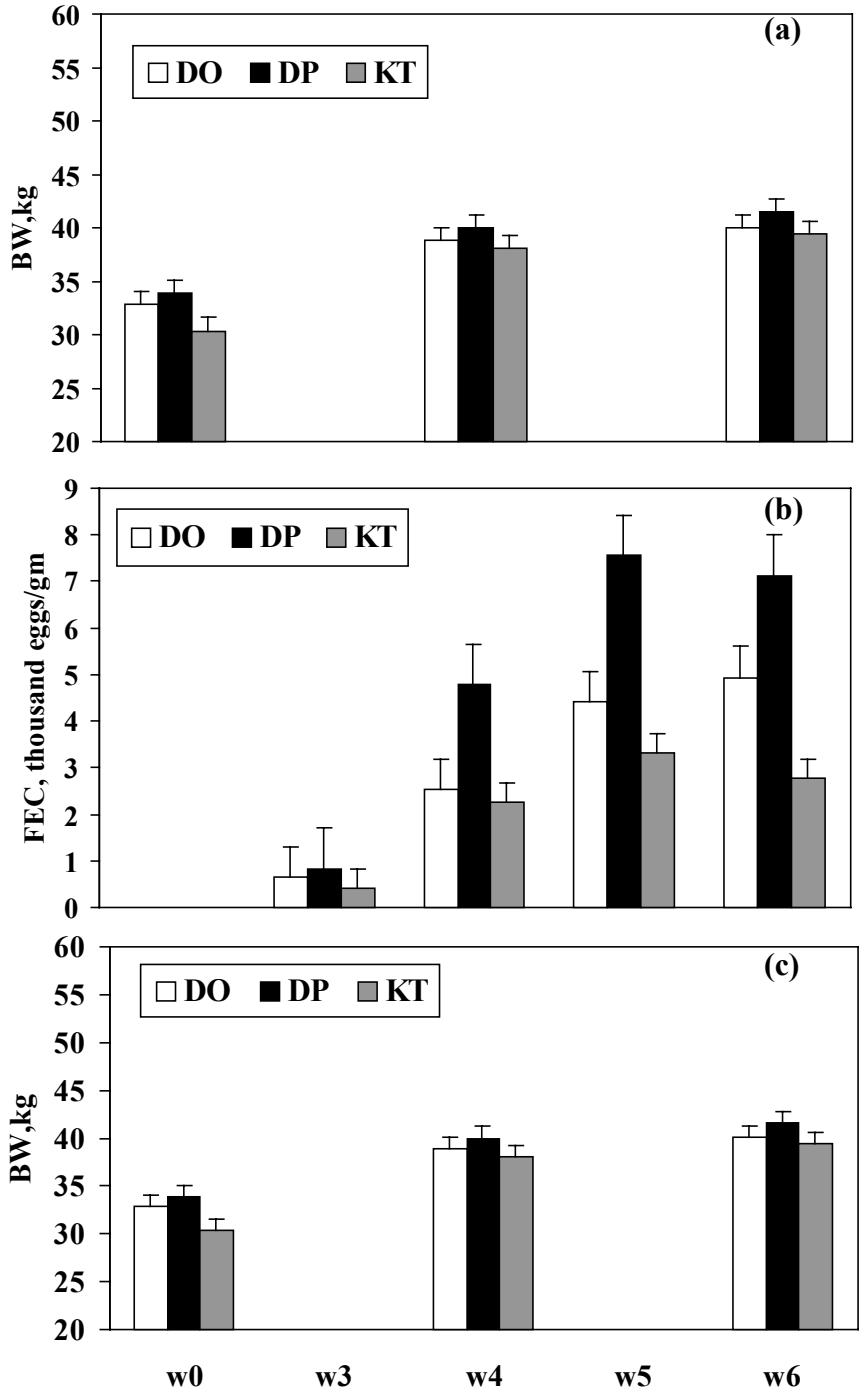

Fig 4.3 Breed x week least square means for: (a) body weight (BW), kg, (b) back transformed log fecal egg count (FEC), eggs/gm, and (c) packed cell volume (PCV), %, in 2002 Dorset (DO), Dorper (DP), and Katahdin (KT) ewe lambs.

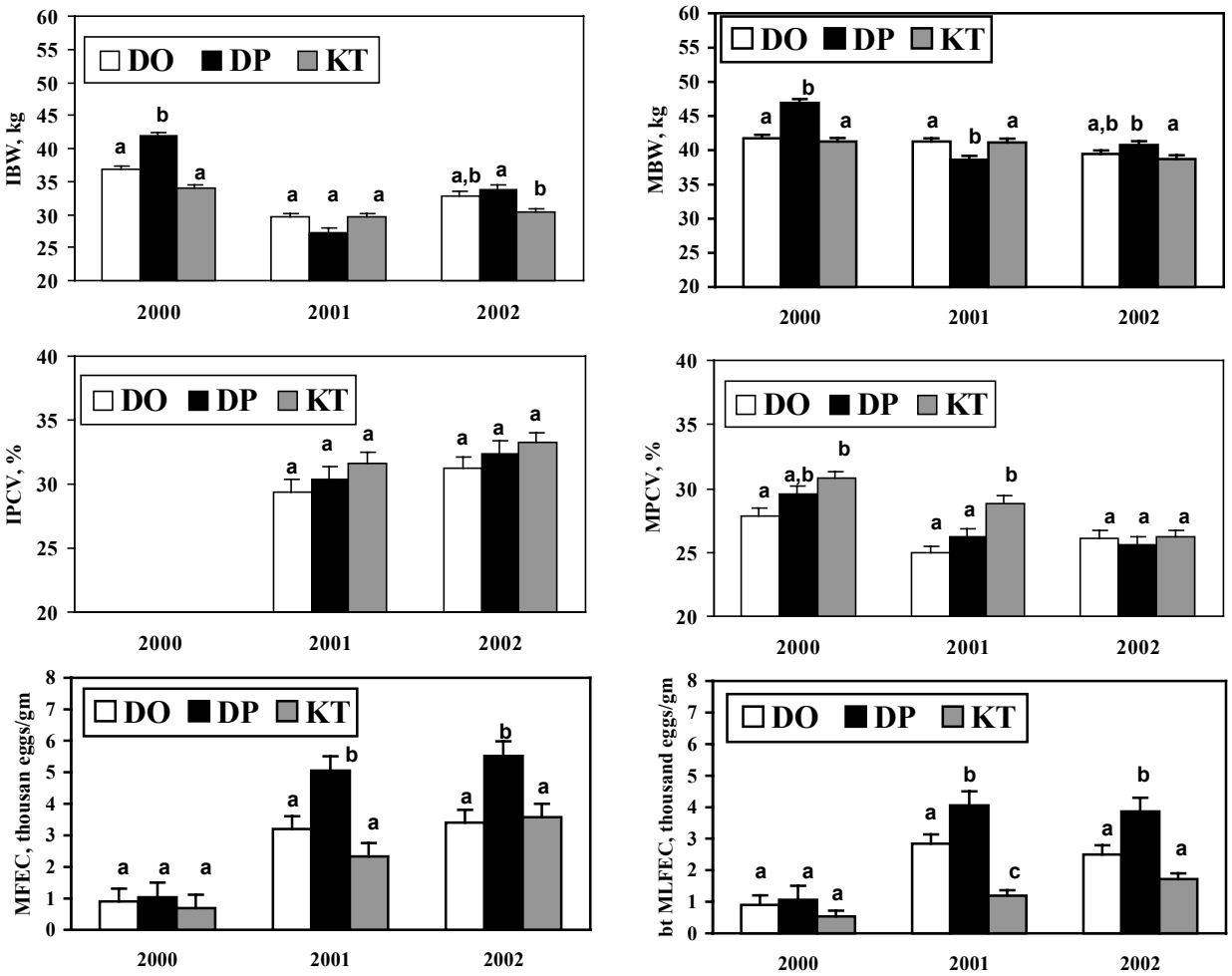

Fig 4.4 Year x breed least square means after adjustment for year x breed initial body weight (except (a)) for: (a) initial body weight (IBW), kg, (b) mean body weight across 4 post-infection measurement times (MBW), kg, (c) initial packed cell volume (IPCV), %, (d) mean packed cell volume across 4 post-infection measurement times (MPCV), %, (e) mean fecal egg counts (MFEC), and (f) back-transformed mean log fecal egg counts (bt MLFEC) across 4 post-infection measurement times, eggs/gm in Dorset (DO), Dorper (DP), and Kathadin (KT) ewe lambs.

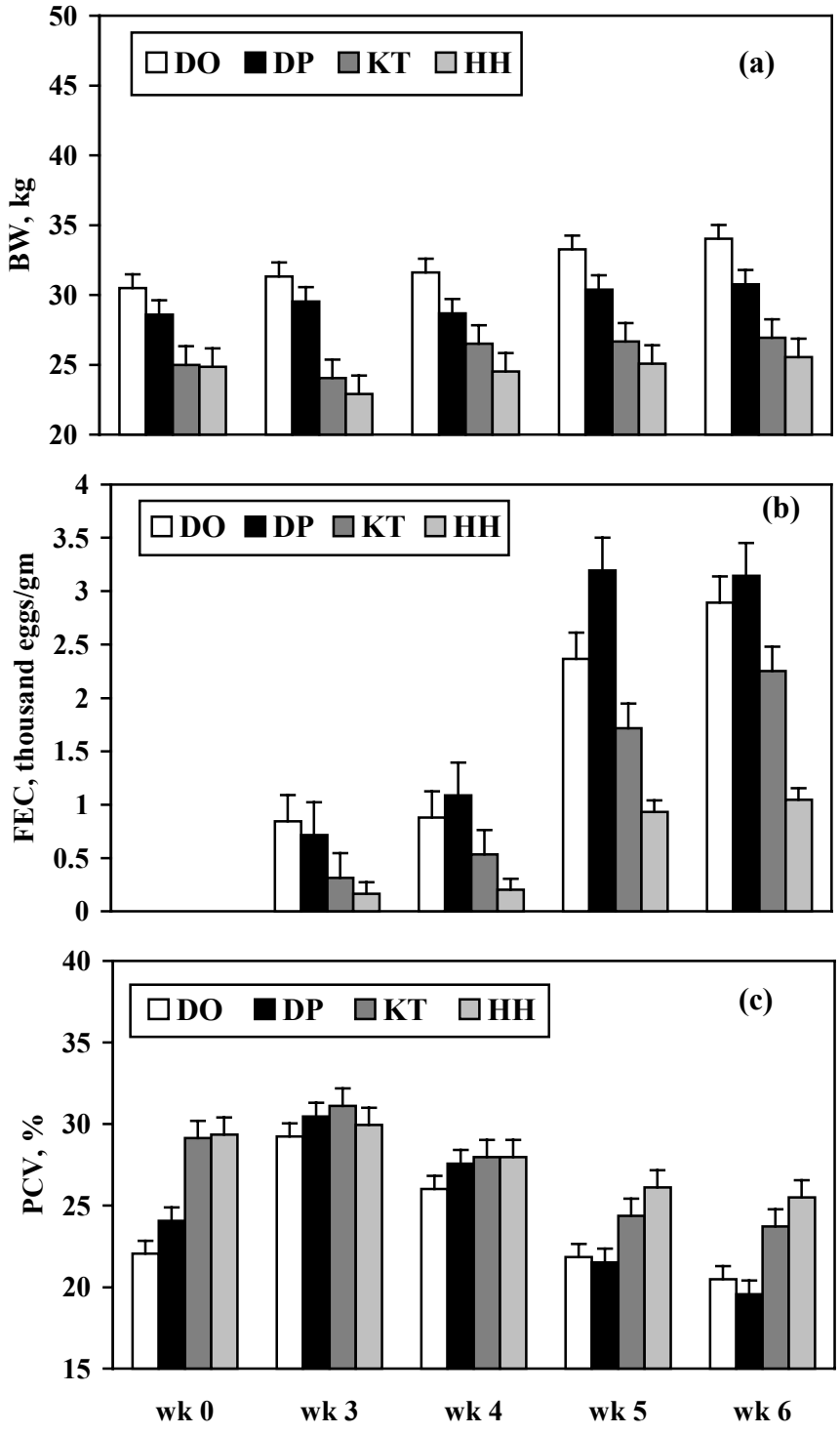

Fig 4.5 Breed x week least square means for: (a) body weight (BW), kg, (b) back-transformed log fecal egg count (FEC), eggs/gm, and (c) packed cell volume (PCV), %, in 2001 Dorset (DO), Dorper (DP), Katahdin (KT), and hair sheep (HH) wethers.

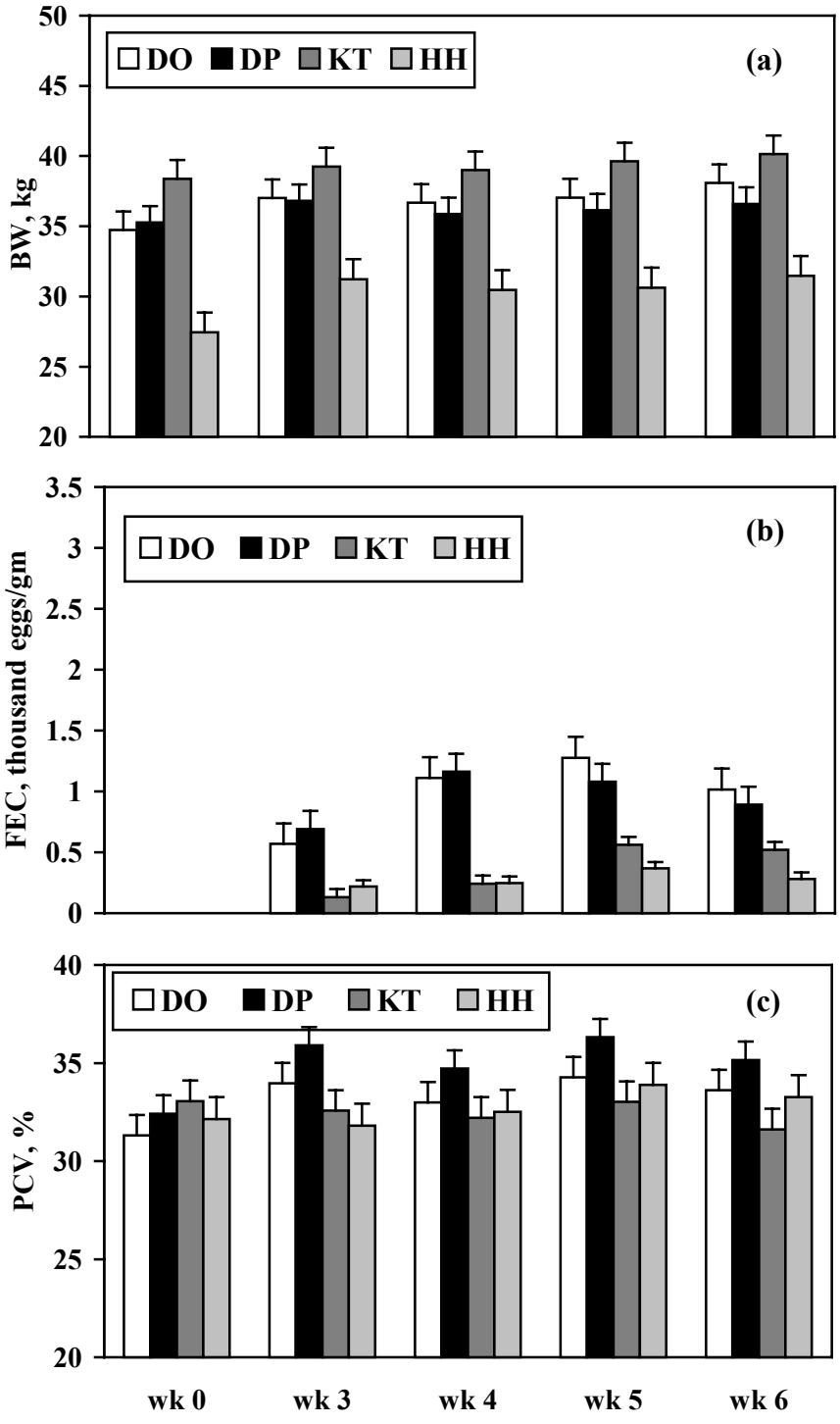

Fig 4.6 Breed x week least square means for: (a) body weight (BW), kg, (b) back-transformed log fecal egg count (FEC), eggs/gm, and (c) packed cell volume (PCV), %, in 2002 Dorset (DO), Dorper (DP), Katahdin (KT), and hair sheep (HH) wethers.

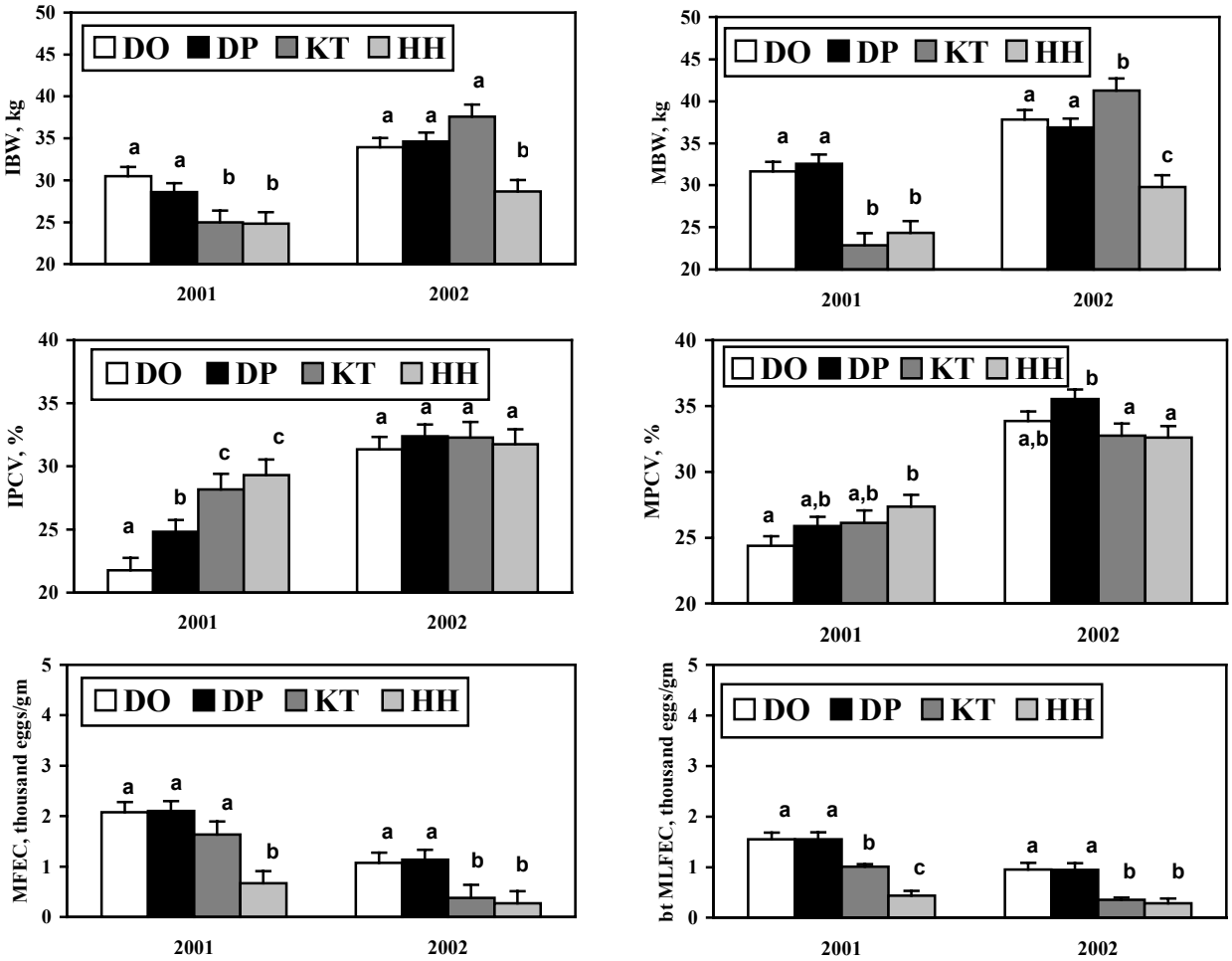

Fig 4.7 Year x breed least square means after adjustment for year x breed initial body weight (except (a)) for: (a) initial body weight (IBW), kg, (b) mean body weight across 4 post-infection measurement times (MBW), kg, (c) initial packed cell volume (IPCV), %, (d) mean packed cell volume across 4 post-infection measurement times (MPCV), %, (e) mean fecal egg counts (MFEC), and (f) back-transformed mean log fecal egg counts (bt MLFEC) across 4 post-infection measurement times, eggs/gm in Dorset (DO), Dorper (DP), Kathadin (KT), and hair sheep (HH) wethers facing a natural pasture challenge.

GENERAL DISCUSSION AND IMPLICATIONS

The protocol used in these experiments allowed adequate assessment of response to *H. contortus* infection in sheep in an intensive production environment, without any observable adverse effects on the condition of the animals. A very small number of lambs (< 3 %) and only two ewes exhibited signs of anemia and had to be removed from the study. Thus, a protocol such as this can be incorporated into a commercial sheep farming enterprise to measure parasite resistance of animals with out causing major production losses or delaying age at first breeding. The data thus obtained can be utilized to generate estimated breeding values (EBV) for parasite resistance to aid in selection of resistant sires and/or dams. Parasite resistance EBV could be used as advantageous tools in marketing of breeding stock, especially in regions where endo-parasitic infections are a major deterrent to sheep production.

Parasite resistance, measured in terms of FEC and PCV during infection, was found to be moderately heritable in both lambs and ewes. Measurements taken at the peak of infection (wk 3 through 5 post-infection) should be sufficient to maximize heritability of FEC in case of lambs. From the results obtained here, a single measurement taken at 3 wk post-infection should result in near maximum response to selection in lambs. Assuming a genetic correlation of -0.86 (Albers et al., 1987) between single measures of FEC and PCV during peak of infection, selection for reduced FEC using a combined index consisting of the most heritable individual FEC and PCV measures during infection (at wk 3 and wk 5 post-infection, respectively, and with heritability estimates of 0.42 and 0.54, respectively; both $P < 0.01$) will produce 10% more genetic gain than selection based on the most heritable FEC measure alone. With a more conservative estimate of -0.65 for genetic correlation between FEC and PCV, a combined index will produce 5% more genetic gain than using FEC alone. It is important to consider if this additional gain in response warrants measurement of PCV in addition to measurement of FEC in a commercial setting given the increased labor and costs involved.

The moderate heritability estimates for FEC and PCV indicate that selection for increased or decreased resistance to *H. contortus* is possible for sheep in this environment and that genetic improvement in parasite resistance levels can be made. Lines of sheep with low and high resistance to *Haemonchus* could be established to study immunological mechanisms of actions involved in parasite resistance and to possibly identify quantitative trait loci associated with resistance to parasites.

The data used in the first experiment were not adequate to obtain genetic correlations between parasite resistance traits and production traits. However, when parasite resistance traits were regressed on EBV for growth potential in lambs, they were found to be favorably associated. Therefore, in lambs, selection for parasite resistance will not adversely affect growth potential and both traits can be improved at the same time. A two-stage selection approach can be used to improve both parasite resistance and growth in lambs by first selecting lambs of good growth performance and then selecting for parasite resistance among those lambs. Also, an index could be formulated involving both growth performance and parasite resistance to select for high-performing, parasite resistant sheep.

In ewes, parasite resistance and reproductive performance were favorably associated. Thus, selection for improved parasite resistance will not adversely affect reproductive performance of ewes and both can be improved together. However, lambs that have higher genetic merit for growth were more susceptible to infection as ewes. Correlations between parasite resistance traits of dams and lambs were generally low and the traits appeared to be controlled by different mechanisms in lambs and ewes. Therefore, genetic improvement of parasite resistance in ewes may require evaluation of their parasite resistance as yearlings or adults.

Breed differences in resistance to gastro-intestinal nematode infections were also observed. Hair sheep and KT were more parasite resistant than DO or DP and could be used in cross-breeding programs to improve resistance levels in high-producing commercial breeds such as Dorset or Suffolk. Hair sheep rams could be mated to domestic ewes such as Dorset or Rambouillet, and KT ewes could be mated to commercial sire breeds, such as Suffolk, to improve parasite resistance of crossbred lambs while maintaining good growth characteristics. Dorper showed much higher FEC than DO, but maintained comparable BW and higher PCV than DO suggesting that DP are less resistant to infection than DO but are probably more resilient or can cope better with infections.

VITA

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