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Grazing systems and worm control in sheep: a long-term case study involving three management systems with analysis of factors influencing faecal worm egg count

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Abstract. Managing infections of sheep with gastrointestinal nematode parasites (worms) and problems of resistance to anthelmintic treatments continue to be major challenges for graziers on the Northern Tablelands of New South Wales, Australia. The whole-farmlet study of grazing enterprises undertaken by the Cicerone Project tested the broad hypotheses that compared with typical management (farmlet B), internal parasites can be more effectively managed with improved nutrition (farmlet A) or by intensive rotational grazing (farmlet C). Further aims were to identify the major sources of variation in faecal worm egg count (WEC) over the 6-year period and to examine the efficacy of the various anthelmintic treatments used during the experiment. This paper describes the management of sheep worms at the whole-farmlet level during the experiment, and analyses data from the routine WEC monitoring (5644 records) and larval differentiation tests (322 records) carried out on behalf of the Cicerone Management Board and by a doctoral candidate. It complements more detailed investigations published elsewhere.

Over the period from July 2000 to December 2006, worm infections in ewes, lambs, hoggets and wethers were, with some exceptions, successfully controlled on the farmlets through a combination of regular monitoring of WEC, treatment with a wide array of anthelmintics and grazing management. Farmlet C had lower mean WEC (444 epg) and annual anthelmintic treatment frequency (3.1 treatments/year) over the whole experimental period than farmlets B (1122 epg, 4.3 treatments/year) or A (1374 epg, 4.7 treatments/year). The main factors influencing WEC were the time since the last anthelmintic treatment, and the anthelmintic used at that treatment. The magnitude of these effects dwarfed those of climatic and management factors that might be expected to influence the epidemiology of gastrointestinal nematode infections via environmental or host-mediated mechanisms. Nevertheless management factors associated with stocking rate and grazed proportion (proportion of each farmlet grazed at any one time), and climatic indicators of both temperature and moisture availability had significant effects on WEC.

The results show that, in a region with *Haemonchus contortus* as the major sheep nematode, improved host nutrition in a higher input system (farmlet A) did not provide more effective control of gastrointestinal nematodes than typical management (farmlet B); however, it was observed that gastrointestinal nematode control was no worse on farmlet A than on farmlet B in spite of farmlet A supporting a 48% higher stocking rate by later in the trial period (2005). The study provided strong support for the proposition that intensive rotational grazing (farmlet C) provides more effective control of gastrointestinal nematodes than typical management (farmlet B) as evidenced by significantly lower WEC counts and anthelmintic treatment frequency. Tactical worm control based on routine monitoring of WEC provided adequate control of worms on all three farmlets for much of the experimental period but failed to prevent significant spikes in WEC to values associated with significant production loss on multiple occasions, and significant ewe mortality on farmlets A and B on one occasion.

Additional keywords: anthelmintic, Haemonchus, integrated parasite management, nutrition, resistance, rotational grazing, Trichostrongylus.

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Introduction

Gastrointestinal nematode (roundworm) parasites of sheep are an ongoing and important problem for graziers on the Northern Tablelands of New South Wales (NSW), Australia. Resistance to anthelmintic drenches is a major and widespread problem that is getting worse (Love 2012). Gastrointestinal worm infection is the most economically important disease of sheep in Australia (McLeod 1995; Sackett *et al*. 2006) and the impact has recently been described in detail for the Northern Tablelands of NSW by Kelly *et al*. (2010). The major worm species in this region are the abomasal *Haemonchus contortus* (Barber's pole worm) and the small intestinal *Trichostrongylus colubriformis* (Black scour worm) with some presence of other species including the abomasal *Teladorsagia circumcincta* (small brown stomach worm). The former induces significant blood loss with the major impact being elevated mortality. The latter two species are 'scour worms', which are associated with lower reproductive rates and a more chronic course of infection leading to reduced production as the major economic impact. Severe infections of any of these worm species can result in animal deaths and these occur most commonly under moist summer conditions (Gordon and Whitten 1941; Roe *et al*. 1959*b*).

As part of the producer-led Cicerone Project (Sutherland *et al*. 2013), a survey of the research needs of livestock producers in this region was undertaken by Kaine *et al*. (2013). This revealed considerable concern about control strategies for sheep intestinal worms and the potential for drench resistance as well as interest in alternative control strategies including that of intensive rotational grazing (IRG). Even though short-term rotational grazing, using weekly rotation across four paddocks, was found not to affect worm burdens (Roe *et al*. 1959*b*), there has been anecdotal evidence of low drenching requirements on some properties practising more IRG or 'cell grazing' with shorter graze and longer rest periods. Producer members of the Cicerone Project were thus keen to compare grazing strategies that used short graze periods and long rest periods with more typical management strategies. A decision was taken by the Cicerone Board to explore several questions, including gastrointestinal worm control, within three whole farmlets that would test strategies at a scale viewed as credible by livestock producers.

Thus, three 53-ha farmlets were established to allow the effects of management differences to be quantified over time. One farmlet (B) was managed as a typical, or control, system based on moderate levels of pasture inputs and soil fertility with eight paddocks and flexible rotational grazing. A second farmlet (A) was managed to have a high level of pasture renovation with a higher level of soil fertility but with the same number of paddocks and grazing management as farmlet B. The third farmlet (C) was subdivided into 17 paddocks and, after a year, into a total of 37 subpaddocks to allow for IRG while receiving the same level of inputs as farmlet B. The management of worms on the farmlets was essentially tactical, based upon regular (approximately monthly) worm faecal egg count (WEC) monitoring of different mobs on the different farmlets. Worm control interventions were made on the advice of an expert veterinary consultant who also sat on the Cicerone Board of Management.

Some of the results of detailed parasitological studies on the Cicerone farmlet experiment have already been published. Healey *et al*. (2004) examined the WEC data for the first 3 years of the experiment and reported that clear farmlet differences emerged in 2003, the third year of the experiment, with the main finding being reduced WEC and frequency of treatment on farmlet C. Colvin *et al*. (2008), using monthly samples from lambs, hoggets and ewes over 2 years (2004–05) on each farmlet, demonstrated that IRG of farmlet C can indeed assist in the control of gastrointestinal nematodosis, especially where *H. contortus* is the most common parasite. A companion paper (Colvin *et al*. 2012) reported that the observed effects of IRG were due to disruption of the parasite lifecycle outside of the host, rather than differences in host immunity. Indeed, sheep on farmlet C were significantly more susceptible to worms than those on farmlets A or B during spring and summer.

As a complement to these detailed studies, this paper provides a longer-term overview of the management of internal worm parasites across mobs of various ages on the three farmlets over the entire 6.5 years of the farmlet experiment. Its main aim is to test two broad hypotheses that producer members of the Cicerone Project wanted investigated at a 'credible' scale. These were that compared with typical management (farmlet B), internal parasites can be more effectively managed with (1) improved nutrition (farmlet A) or (2) by IRG (farmlet C). Further aims were to identify the major sources of variation in WEC over the experimental period and to examine the efficacy of the various anthelmintic treatments used.

Materials and methods

Experimental design and location

The background to the Cicerone Project and its design are detailed by Sutherland *et al*. (2013) and Colvin *et al*. (2008). Briefly the farmlet experiment was located on the CSIRO property, 'Chiswick', 18 km south of Armidale, NSW, Australia (950 m altitude 30°31′S, 151°39′E). Armidale has a cool, temperate climate with the majority of rain falling in the summer months. Winters are generally dry, cold and frosty with occasional light snowfall. Summer days are warm but nights are generally cool. The average annual rainfall is ~790 mm. The weather experienced during the trial period was mostly drier than average with more severe frost in winter than average (Behrendt *et al*. 2013). The farmlet experiment commenced on 1 July 2000 following the subdivision of the three farmlets, each of 53 ha, which were managed under three different management systems described in detail by Scott *et al*. (2013*b*). Stock was first introduced just before the start date and the experiment was completed by the end of 2006.

This paper encompasses a longitudinal study of WEC between January 2001 and May 2006 under the three management systems described in the Introduction. The key factors in the design were:

- Three farmlets each representing a different management system: farmlet A (higher inputs), farmlet B (typical) and farmlet C (IRG).
- Four classes of sheep: lambs (0–12 months), hoggets (~12–24 months), mature ewes and wethers.
- Year and season. Years were calendar years and seasons were spring (Sept.–Nov.), summer (Dec.–Feb.), autumn (March–May) and winter (June–Aug.).

Sheep, management and worm control

All sheep were fine wool Merinos. Ewes were generally mated for 5 weeks in mid–late autumn to lamb in spring. Lamb marking was generally in mid November and weaning from late December to January. Shearing of all sheep took place at the end of July each year in an off-site shearing shed. Managing worm burdens was largely tactical, based upon WEC testing at 1–2-month intervals of the various sheep classes on the different farmlets, followed by larval culture and differentiation to species or genus level is a common practice in this region. In addition, two fixed treatments were given each year: the first was a quarantine treatment given to all sheep as they moved off the property for shearing in July and the second was a pre-mating treatment for all ewes in March–April before being grouped together in a paddock external to the experimental farmlets over the joining period, to ensure equivalent genetics between farmlets. Interpretation of the WEC and larval differentiation data and decisions about treatment and the anthelmintic to be used were made by a Veterinary consultant (E. Hall) in consultation with the Cicerone Board of Management where necessary. A wide range of anthelmintic treatments was used as summarised in Table 1; all were used according to the manufacturers' recommendations.

Measurements

Individual faecal samples were either collected per rectum (May 2002–November 2003) or collected from each mob by mustering the mob into a paddock corner and waiting for defecation followed by collection of fresh samples from the ground. Ten individual faecal samples, considered adequate by Morgan *et al.* (2005), were sent to one of three laboratories (Laboratory A, August 2000–May 2002; Laboratory B, May 2002–November 2003 and after October 2005; Laboratory C, November 2003–October 2005) for assessment of WEC using a modified McMaster method (Whitlock 1948). The remaining faeces were pooled, cultured for 7 days followed by L_3 recovery and differentiated into species (*H. contortus*, *Teladorsagia circumcincta*) or genus (*Trichostrongylus*, *Oesophogostomum* or *Cooperia*) in the same laboratory. The total number of WEC records was 5644 and the number of larval differentiations was 322.

A faecal egg count reduction test (FECRT) was carried out on farmlet C lambs in May 2004 to determine the effectiveness of four anthelmintics against *H. contortus*. Due to the small number of lambs available, only four treatment groups plus a control group were used. The control lambs were sampled at the beginning and the end of the experiment to determine the change of WEC over time and FECRT was calculated using the method of Kemper and Walkden-Brown (2004). The FECRT commenced when the WEC of the lambs reached a threshold of 400 eggs/g testing the following anthelmintics: albendazole (3.8 mg/kg Alben, Virbac, Australia), levamisole (8.0 mg/kg, Levamisole Gold, Virbac, Australa), ivermectin (0.2 mg/kg Ivomec Oral Sheep Liquid, Merial, Australia), closantel (7.5 mg/kg, Closicare, Virbac, Australiag) at full dose rate. On Day 0, 75 lambs were randomly allocated to five groups of 15, all lambs were sampled for individual faecal WEC and pooled group larval cultures, bodyweights were recorded and each lamb dosed using a stomach tube, with the correct dose of anthelmintic, or 30 mL of water for the control group. On Day 13 individual WEC and group cultures were carried out and faecal WEC reduction calculated for *H. contortus* as this was the only nematode for which WEC was sufficient to enable accurate determination of FECR. The presence of resistance to an anthelmintic was assumed if (i) the percentage reduction in WEC was less than 95% and (ii) the lower 95% confidence interval was less than 90%. Emerging resistance was suspected when only one of these criteria was met (Coles *et al.* 1992).

Rainfall and temperature data were accessed from the nearest Bureau of Meteorology station (Armidale) some 17 km north of the experimental site. As described in a related paper by Behrendt *et al.* (2013), the climate experienced over the experimental period was in general drier than average, especially over the autumn–spring period, and experienced more severe frosts than average. Climatic data over the long-term from 1890 to 2008 were used as inputs to the model *Ausfarm*, which permitted the estimation of changes in available soil water (ASW) over both the long-term and the experimental period (Behrendt *et al.* 2013). The same climatic data were used to estimate the potential effects of temperature on gastrointestinal nematodes and pasture growth as the average of growing-degree days (GDD) calculated using base temperatures of 4°C for grasses and 10°C for clovers [((max. temp + min. temp)/2) – (base temp)] (Hutchinson *et al.* 2000).

Statistical methods

WEC data were not normally distributed and so were treated in two ways. To illustrate general patterns and trends, untransformed means are presented as this is the format in which the farming and advisory community receive and have to interpret such data. In addition to this descriptive presentation, formal analyses of WEC

Table 1. Details of the drenches and combinations of drenches used on farmlets A, B and C over the duration of the trial from July 2000 to December 2006

Drench types and combinations	Abbreviation	Length of action	Spectrum
Abamectin	AB	Short	Broad
Abamectin + BZ[A] + LEV[B]	ABL	Short	Broad
BZ + LEV	BL	Short	Broad
Closantel	C	Medium	Narrow
LEV	L	Short	Broad
LEV + Closantel	LC	Short	Broad
LEV-Double	L2	Short	Broad
LEV-Double + Closantel	L2C	Medium	Broad
Moxidectin	M	Medium	Broad
Moxidectin LA[C]	Mla	Long	Broad
Moxidectin + BZ + LEV	MBL	Medium	Broad
Moxidectin + Ivermectin	MI	Medium	Broad
Moxidectin + Napthalophos + BZ + LEV	MNBL	Medium	Broad
Napthalophos + BZ + Closantel	NBC	Medium	Broad
Napthalophos + BZ	NB	Short	Broad
Napthalophos + BZ + LEV	NBL	Short	Broad

[A]Benzimidazole.
[B]Levamisole.
[C]Long-acting.

were carried out to explore the sources of variation in this variable and their contribution to total variation. For these analyses WEC was transformed [Log_{10} (WEC + 20)] (LogWEC) before fitting least-squares models as this transformation best stabilised the variances and distribution of the residuals. WEC data were coded by a range of fixed and variable effects as shown in Table 2.

For this analysis all data from wethers and the years 2000 and 2006 were excluded as they were sparse and not well balanced across the other fixed effects. This reduced the number of WEC samples analysed from 5644 to 5183. The importance of various factors in the WEC models was evaluated by their contribution to the R^2 value for the model; that is, their contribution to total sums of squared deviations from the mean (SSQ).

Larval differentiation data (% of each genus) are presented without formal analysis. Annual drench frequency was calculated within classes, farmlets and years on the reduced dataset and analysed by fitting these effects and their two-way interactions in a least-squares model.

All analyses were performed using JMP 10 statistical software (SAS Institute, Cary, NC, USA) and a significance level of $P < 0.05$ has been used throughout.

Results

Mean length of graze and rest periods

The relative lengths of graze and rest periods on each farmlet over each year of the trial are shown in Table 3 as averages over all major paddocks and subpaddocks on each farmlet. The mean number of graze days were lower on farmlet A than on farmlet B, due presumably to the higher level of green digestible herbage (Shakhane *et al*. 2013) and stocking rate (SR, Hinch *et al*. 2013*a*) on this farmlet with both of these farmlets having substantially longer graze periods than on farmlet C. The lengths of the grazing rest periods were similar on both farmlets A and B but were some 50% longer on farmlet C. It should be noted that, as grazing on farmlet C was usually within 'cells', which were smaller than subpaddocks, the actual days of grazing on this farmlet were lower and the days of rest higher than indicated in Table 3.

Mean percentage of farmlets grazed

Fig. 1 shows the mean percentage of each farmlet grazed together with the daily rainfall over the experimental period. After the grazing treatments were implemented in late 2000, the percentage of farmlets A and B grazed at any one time varied from 20 to 40% whereas that of farmlet C varied from ~5 to 10%.

Mean faecal WEC within sheep classes and farmlets over time

Untransformed mean WEC by farmlet over the experimental period are shown in Fig. 2 (ewes and lambs) and Fig. 3 (hoggets and wethers). These data show clearly that major spikes in WEC occurred on farmlets A and B in 2003, 2004 and 2005, but that such extreme fluctuations in WEC were not evident on farmlet C. WEC on farmlets A and B tended to be somewhat higher than those on farmlet C except in early 2006 when farmlet C ewes had the highest counts following a period of shorter rest days.

Overall raw mean WEC for farmlets A, B and C over the entire experimental period were 1374, 1122 and 444, respectively, for ewes; 1162, 910 and 419, respectively, for lambs; 974, 879 and 372, respectively, for hoggets; and 800, 585 and 291, respectively, for wethers. Over all years and classes the mean WEC for farmlets A, B and C were 1178, 985, 415, respectively.

Table 2. List of fixed effects and covariates used in the analysis of LogWEC

Factor or covariable	Abbreviation	Levels	Description
Farmlet	Farmlet	3	Farmlets A, B or C
Class	Class	4	Lambs, hoggets, mature ewes, wethers
Year	Year	6	2001, 2002, 2003, 2004, 2005, 2006
Season	Season	4	Spring (Sept.–Nov.), summer (Dec.–Feb.), autumn (March–May) and winter (June–Aug.)
Last anthelmintic treatment code	TC	18	Anthelmintics defined by active principle alone and in mixtures (see Table 1)
Days since last anthelmintic treatment	DSLT	Cov.[A]	–
Minimum, maximum and mean temperatures (°C)	T_{MIN}, T_{MAX}, T_{MEAN}	Cov.	Means of each value for the 30 days before sampling
Growing-degree days	GDD	Cov.	Mean of the growing-degree days calculated for each of the 30 days before sampling
Rainfall (mm)	RAIN	–	Sum of rainfall for the 30 days before sampling
Available soil water index (0–1)	ASW	Cov.	Mean modelled available soil moisture for the 30 days before sampling
Evaporation rate (mm)	EVAP	Cov.	Sum of daily evaporation rate for the 30 days before sampling
Precipitation/Evaporation ratio	P/E	Cov.	RAIN/EVAP
Stocking rate (DSE/ha)	SR	Cov.	Mean farmlet stocking rate (DSE/ha) for the 30 days before sampling (Hinch *et al*. 2013*a*)
Grazed proportion	GP	Cov.	Mean proportion of area of farmlet grazed relative to total area of each farmlet over the 30 days before sampling

[A]Covariable with a continuous distribution.

Over all years and farmlets, the mean WEC for ewes, lambs, hoggets and wethers were 988, 846, 735 and 666, respectively.

Nematode genera involved

For the 322 recorded larval differential tests carried out during the experiment, the overall means for genus identification were 66.4% *Haemonchus*, 23.1% *Trichostrongylus*, 8.2% *Teladorsagia*, 2.1% *Oesophagostomum* and 0.2% *Cooperia*. These varied with time and farmlet as shown in Fig. 4. In the early stages of the experiment, *Trichostrongylus* was the dominant parasite, but it declined rapidly as *Haemonchus* increased and, by 2002, *Haemonchus* had become dominant. Farmlet C had a higher proportion of *Teladorsagia* than the other farmlets throughout the experiment and a lower proportion of *Haemonchus* and higher proportion of *Trichostrongylus* than farmlet B in all years apart from 2000 (Fig. 4). Farmlet B had a higher proportion of *Haemonchus* and lower proportion of *Trichostrongylus* than farmlet A in years other than 2003 and 2004 when they were similar. Proportions of *Teladorsagia* were similar in these two farmlets (Fig. 4).

Table 3. Mean annual length of graze and rest periods across all subpaddocks of farmlets A (eight major paddocks + two subpaddocks), B (eight major paddocks + two subpaddocks) and C (17 major paddocks and 20 subpaddocks) from 2000 to 2006

Year	Length of graze periods (days)			Length of rest periods (days)		
	A	B	C	A	B	C
2000	25	23	13	56	55	60
2001	46	71	14	63	72	102
2002	49	94	11	52	65	140
2003	55	80	10	43	54	89
2004	58	81	8	93	51	76
2005	54	60	11	66	88	114
2006	42	119	8	73	78	107
Mean	47	75	11	64	66	98

Frequency of anthelmintic treatment

The number of anthelmintic treatments by year, sheep class and farmlet for the core dataset between 2001 and 2005 are summarised in Table 4. Overall lambs had significantly more annual treatments (4.4) than hoggets (3.4) with ewes having an intermediate level of treatment (4.0), with some year-to-year variation (Table 4).

Types of anthelmintic treatment used and WEC following treatment

The types of anthelmintic used between 2001 and 2005 in ewe, lamb and hogget mobs and their frequency of use by year are shown in Table 5. The number of treatments is slightly higher than might be inferred from Table 4 because on a small number of occasions different mobs within a class of sheep on a farmlet were treated with different anthelmintics on the same day or week. These would represent a single treatment in Table 4 but two treatments in Table 5. The anthelmintics used varied over time with the broad spectrum combination drenches MBL and NB being the most commonly used, largely for the quarantine drenches, followed by the single active L and M.

Examination of WEC profiles following treatment with various anthelmintics failed to show widespread anthelmintic resistance, apart from closantel, for which significant *Haemonchus* WEC were often observed within the projected WEC-free period for this *Haemonchus*-specific anthelmintic

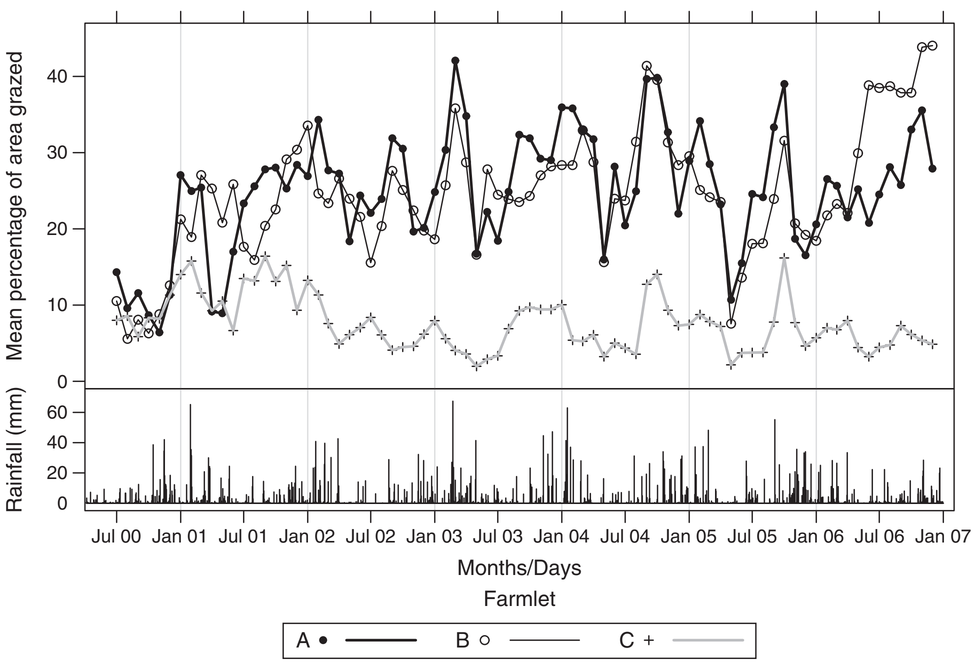

Fig. 1. Monthly mean percentage of each farmlet grazed at any one time between July 2000 and December 2006. Lower panel shows daily rainfall over the same period.

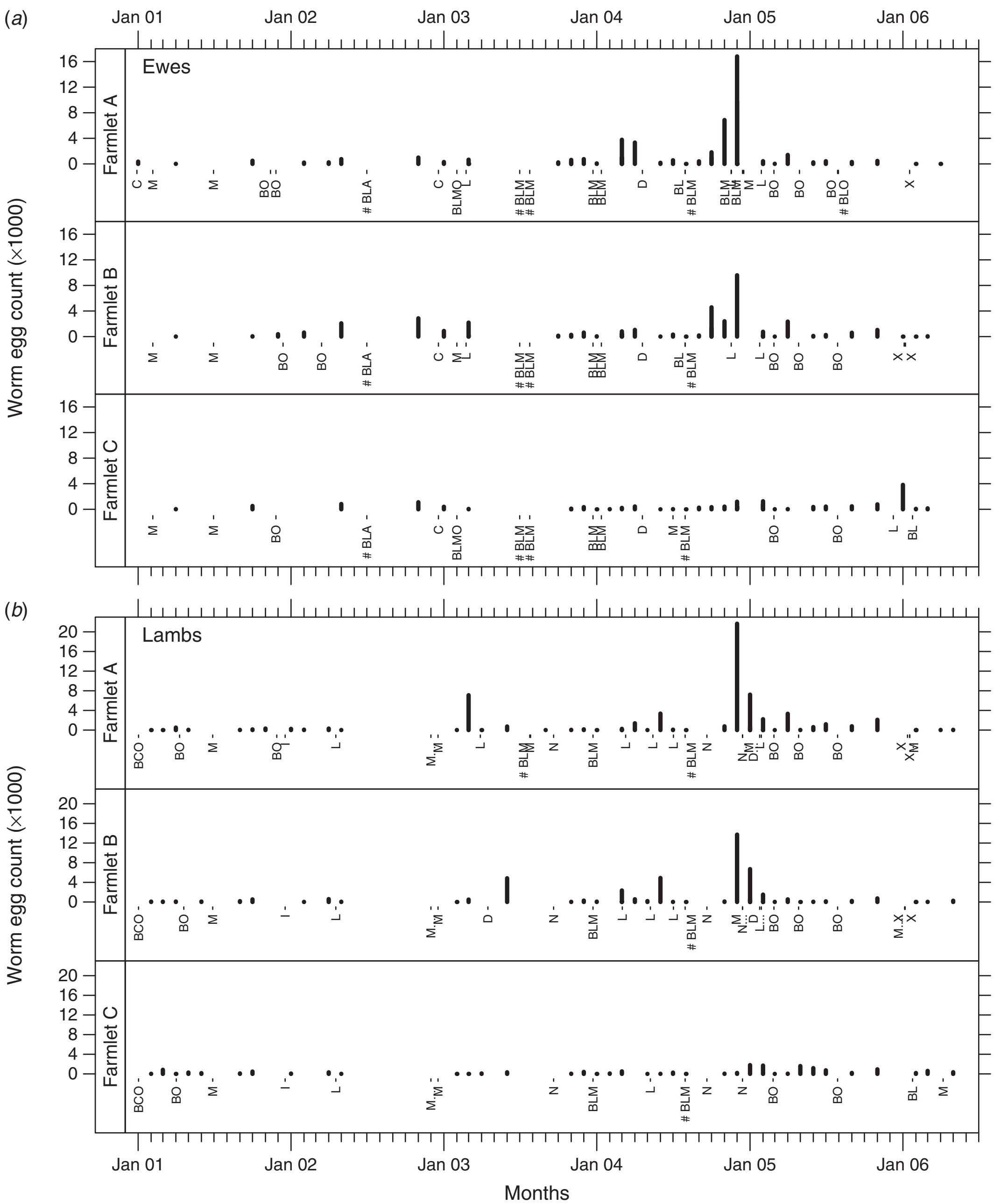

Fig. 2. Mean untransformed worm egg counts counts for (*a*) ewes and (*b*) lambs by farmlet over the course of the experiment. Letters and tick marks indicate anthelmintic treatments while those marked '#' were quarantine drenches for sheep from all farmlets.

(Fig. 5). At the commencement of the faecal WEC reduction test in 2003 on farmlet C mean WEC of the 75 lambs was 817 epg with larval differentiation of 92.6% *Haemonchus*, 3.4% *Trichostrongylus* and 4% *Teladorsagia*. Thus FECRT could only be calculated for *Haemonchus*. Levamisole was the only anthelmintic treatment that returned a 100% susceptibility of *H. contortus* (Table 6). Closantel, which was suspected to have reduced efficacy against this parasite showed efficacy of 96.8% at Day 13 after treatment. Closantel is a persistent anthelmintic with a recommended protection period against *H. contortus* of 42 days, thus emergence of resistance is suspected as there was breakthrough WEC only 13 days after treatment. *Haemonchus contortus* showed resistance to both ivermectin and albendazole.

Sources of variation in WEC and their magnitude

A basic linear model fitting the effects of farmlet, class, year and season and their first-order interactions (Model 1) accounted for only 12.3% (R^2) of the variation in LogWEC during the experiment with an Akaike information criterion (AIC) of

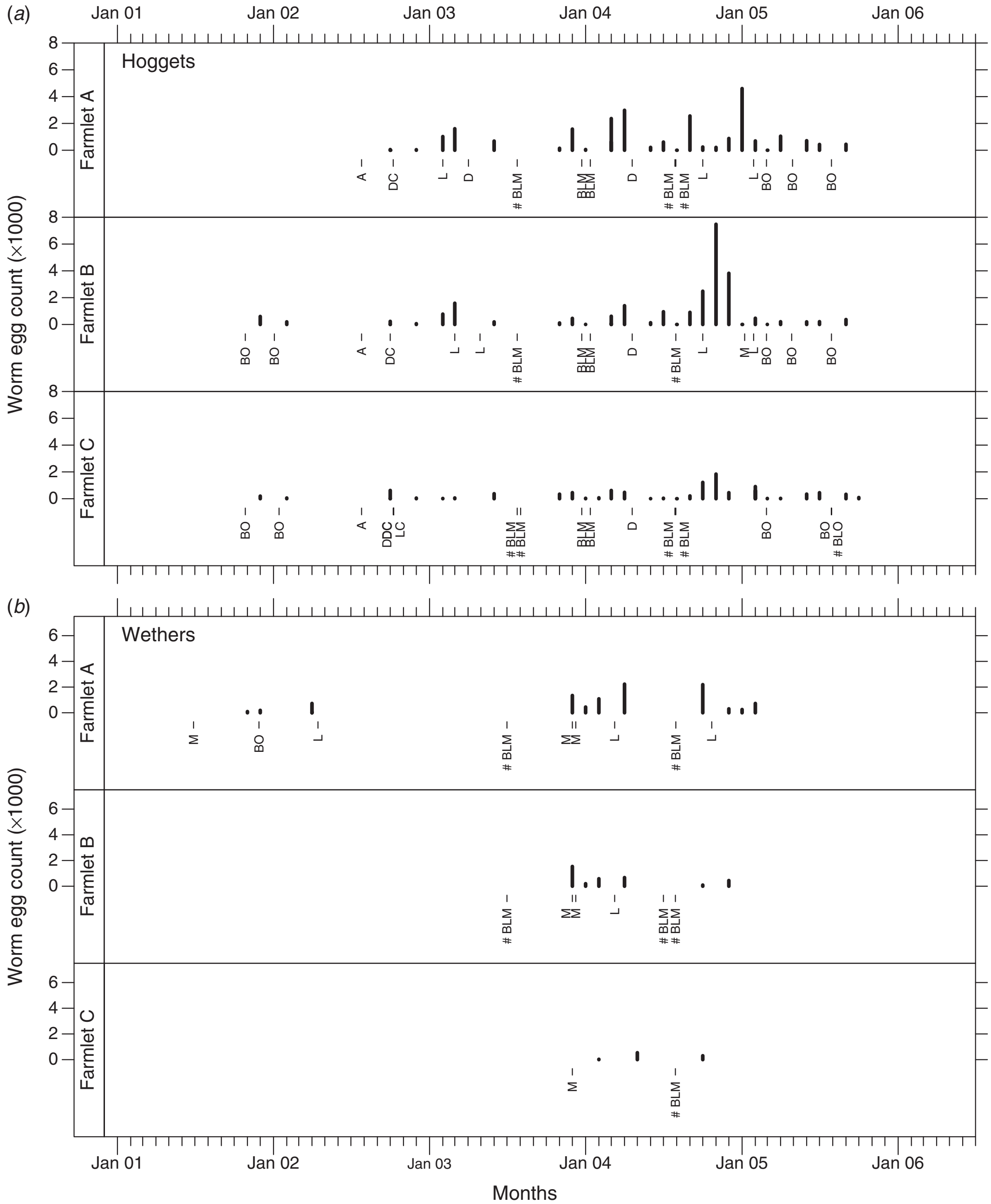

Fig. 3. Mean untransformed worm egg counts counts for (*a*) hoggets and (*b*) wethers by farmlet over the course of the experiment. Letters and tick marks indicate anthelmintic treatments while those marked '#' were quarantine drenches for sheep from all farmlets.

11 981. All effects and first-order interactions were statistically significant ($P < 0.05$), apart from the main effect of farmlet. Addition of the last anthelmintic treatment code (TC) to the model (Model 2) increased the R^2 to 22.2% and further addition of the days since last anthelmintic treatment (DSLT) as a covariate (Model 3) increased the R^2 to 34.3% with an AIC of 10 484. Interactions with these latter two effects were not fitted. In the last of these models all effects and first-order interactions were highly significant ($P < 0.001$) other than the interaction between farmlet and sheep class. The major sources of variation explained by the model were DSLT (18%), TC (11.5%), year (5.1%), class by year (3.5%), class by season (2.7%), season (1.2%) and farmlet by year (1.1%) with all other effects in the model accounting for less than 1% of the total sums of squares. The overall effect of year ($P < 0.0001$) was due to significantly higher LogWEC in 2004 (2.50) than all other years, and significantly higher LogWEC in 2005 (2.20) than 2001 (1.91), 2002 (1.75) and 2003 (1.81), which did not differ among themselves. The overall effect of class was due to significantly higher LogWEC in hoggets (2.23) than both lambs

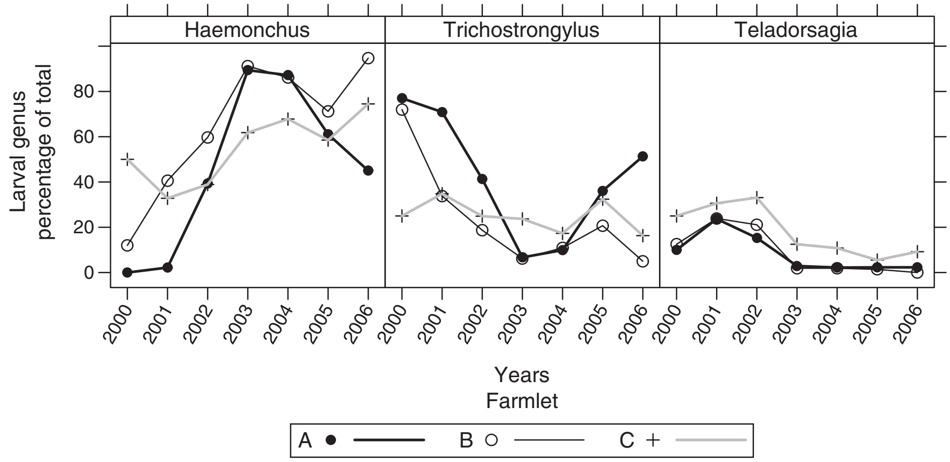

Fig. 4. Mean percentage of *Haemonchus*, *Trichostrongylus* and *Teladorsagia* larvae cultured from faeces during the experiment, by farmlet and year. A total of 322 cultures were performed on pooled faecal samples within sheep class and farmlet.

Table 4. Number of anthelmintic treatments by farmlet, class of sheep and year in the reduced dataset
Main effects followed by different letters are significantly different ($P < 0.05$). n.a., not applicable

Class	Farmlet	2001	2002	2003	2004	2005	Mean
Ewe	A	5	2	5	6	5	4.6
Lamb	A	5	3	6	7	6	5.4
Hogget	A	n.a.	2	5	5	4	4
Mean	A	5.0	2.3	5.3	6.0	5.0	4.7a
Ewe	B	3	3	5	4	6	4.2
Lamb	B	4	3	3	7	6	4.6
Hogget	B	1	4	5	4	6	4
Mean	B	2.7	3.3	4.3	5.0	6.0	4.3a
Ewe	C	3	2	4	5	2	3.2
Lamb	C	4	3	2	4	3	3.2
Hogget	C	1	4	3	4	2	2.8
Mean	C	2.7	3.0	3.0	4.3	2.3	3.1b
Mean	All	3.3c	2.9c	4.2b	5.1a	4.4ab	3.0

Table 5. Type of anthelmintic treatment administered during the experiment by year in the reduced dataset

Anthelmintic[A]	2001	2002	2003	2004	2005	Total
AB	–	3	–	–	–	3
ABL	–	3	–	–	–	3
BL	–	–	–	2	–	2
C	–	3	–	–	–	3
L	–	3	7	11	7	28
L2	–	1	2	6	2	11
L2C	–	5	–	–	–	5
LC	–	1	–	–	–	1
M	9	6	2	6	1	24
MBL	–	–	22	20	–	42
Mla	3	–	–	–	–	3
MNBL	–	–	2	–	–	2
NB	11	3	–	–	29	43
NBC	3	–	–	–	–	3
NBL	–	–	–	–	2	2
NT	–	–	3	6	–	9
Total	26	28	38	51	41	184

[A]Anthelmintic codes. Combinations indicated by multiple codes. AB – oral abamectin, B – oral benzimidazole oral, L – oral levamisole, C – closantel, L2 – double dose of levamisole, M – oral moxidectin, Mla – long-acting injectable moxidectin, N – napthalophos (organophosphate), NT – not treated (before sampling).

(1.96) or ewes (1.91). The overall effect of season was due to significantly ($P < 0.0001$) lower LogWEC in winter (1.82) than all of the three other seasons, spring (2.12), summer (2.10) or autumn (2.10). The overall effect of farmlet was due to significantly ($P < 0.0001$) lower LogWEC on farmlet C (1.89) than farmlets B (2.11) or A (2.10). However, there was significant interaction between the effects of farmlet and year ($P < 0.0001$) with the lower LogWEC on farmlet C only being evident in 2003, 2004 and 2005. Farmlet A also had significantly lower LogWEC than farmlet B in 2002 only.

To test whether actual measures of temperature, rainfall and evaporation would explain more of the variation than the broad category ‘season’, various combinations of actual and derived measures were used in place of season in Model 1. Replacing season with mean temperature (T_{MEAN}) and sum of rainfall (RAIN) over the preceding 30 days increased the Model 1 R^2 marginally from 12.3 to 13.1% (Model 4). Replacing T_{MEAN} with mean minimum temperature (T_{MIN}) did not alter the R^2 (13.1%), but replacing it with the mean maximum temperature (T_{MAX}) increased it slightly to 13.6%. Including both T_{MIN} and T_{MAX} increased the R^2 to 20.4%. Replacing T_{MEAN} with the mean of GDD over the preceding 30 days had little effect on the Model 4 R^2, increasing it marginally to 13.3%. Thus, inclusion of both T_{MIN} and T_{MAX} in place of season provided the best fit of data with regard to temperature.

On the moisture side, replacing RAIN in Model 4 with mean evaporation rate over the preceding 30 days (EVAP) increased the R^2 of Model 4 from 13.1 to 14.6%. Inclusion of both RAIN and EVAP increased it further to 19.1%, but

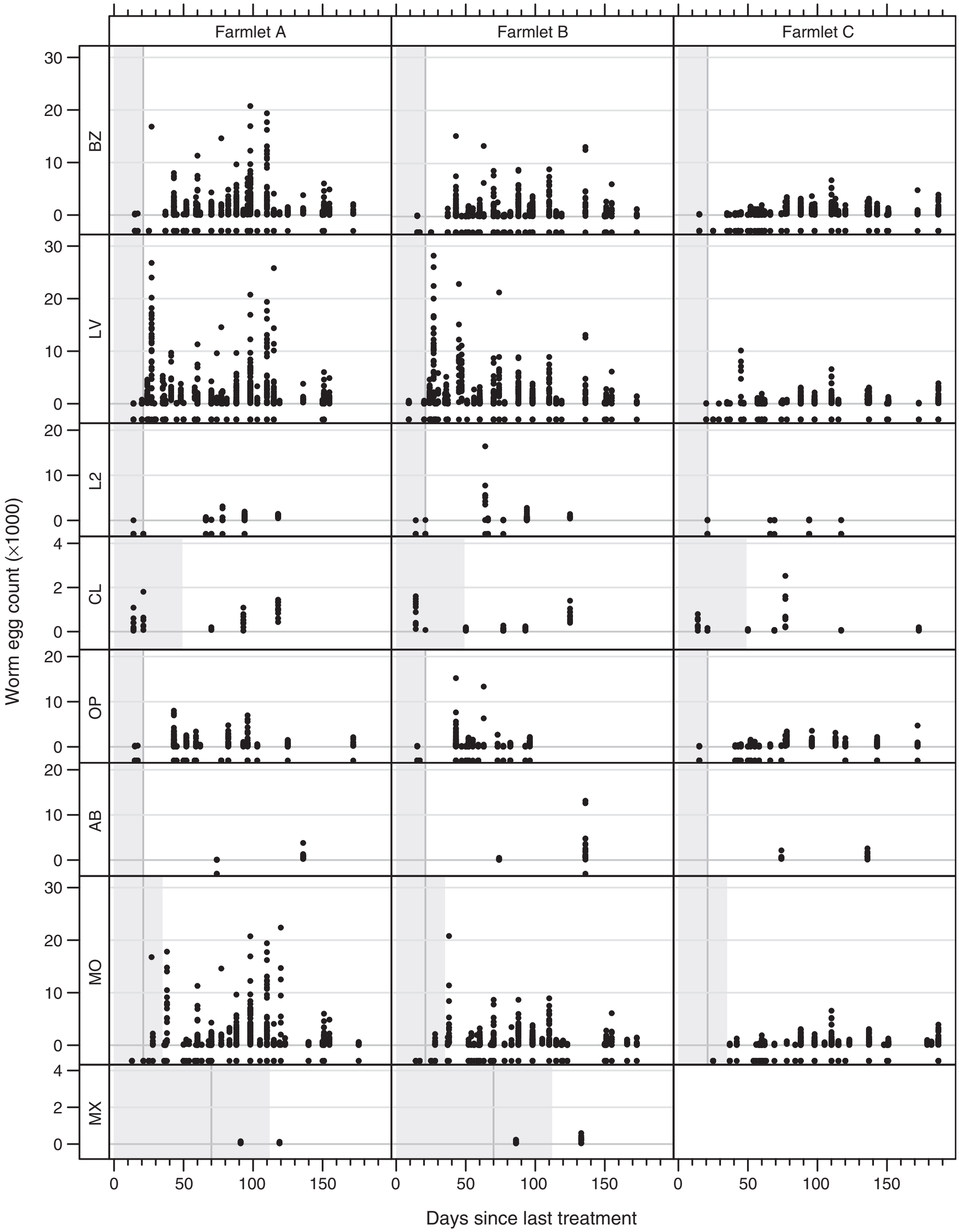

Fig. 5. Worm egg counts (WEC) values by day since previous treatment with specific anthelmintic classes (alone or in combination). Values below the zero line are true zeros. Those apparently on the line are close to zero. Shaded areas indicate predicted WEC-free period for *Haemonchus contortus* if the anthelmintic is fully effective. Grey vertical lines indicate the predicted WEC-free period for *Trichostrongylus.* BZ – oral benzimidazole oral, LV – oral levamisole, L2 – double dose of levamisole, CL – closantel, OP – organophosphate (napthalophos), AB – oral abamectin, MO – oral moxidectin, MX – long-acting injectable moxidectin.

replacing them with the Precipitation/Evaporation ratio over the preceding 30 days (P/E) resulted in a decline in R^2 to 12.3%. Replacing RAIN with modelled available soil moisture for the 30 days before sampling (ASW) increased the R^2 to 14.7%. Thus inclusion of both RAIN and EVAP in place of season provided the best fit of data with regard to moisture.

To test whether actual measures of SR and grazed proportion (GP) for the 30 days before sampling would explain more of

Table 6. Reduction of *Haemonchus* worm egg count (WEC) and lower 95% confidence interval for each anthelmintic treatment used in the faecal egg count reduction test on farmlet C in 2003

	Levamisole	Ivermectin	Closantel	Albendazole
Percent reduction of WEC	100	86.1	96.8	61.1
Lower 95% confidence interval	100	80	93	34

the variation in LogWEC than the broad effect of 'farmlet', the effect of farmlet was replaced by combinations of these variables in Model 1. Replacement of 'farmlet' by SR and GP on their own had little effect on Model 1 R^2 (R^2 of 12.4 and 11.6%, respectively), but inclusion of both, increased the R^2 to 15.0%.

A final model (Model 5) based on Model 3 but replacing farmlet with SR and GP, season with T_{MIN}, T_{MAX}, RAIN and EVAP had an R^2 of 36.4% and AIC of 10 360. Thus only a marginal improvement in R^2 (from 34.3 to 36.4%) was obtained by replacing the generic effects 'Farmlet' and 'Season' with measured variables that may have been expected to capture more relevant information about factors influencing WEC in sheep than these. In Model 5, all of the main effects were statistically significant with the exception of T_{MIN} and RAIN but these, as with other main effects were involved in numerous significant two-way interactions. Removal of interactions reduced the R^2 to 27.3%.

In Model 5 the main sources of variation were TC (6.6% of SSQ, $P < 0.0001$) and DSLT (6.9% of SSQ, $P < 0.0001$), with a strong positive association between DSLT and LogWEC. The effect of TC was difficult to interpret with levamisole, benzimidazoles and closantel in various combinations associated with both high and low LogWEC. The organophosphate napthalophos tended to be associated with lower WEC as did moxidectin, both oral and injectable. The overall effects of SR and GP were highly significant ($P < 0.0001$) and after the anthelmintic-associated effects, accounted for the largest proportion of variation among the main effects (0.82 and 0.92% of SSQ, respectively). In both cases the association with LogWEC was positive. Regression of the Model 5 predicted Log_{10} WEC against SR and GP and resulted in the following linear regression equations:

$$\text{Predicted } Log_{10} \text{ WEC} = 2.049 + 0.657 * GP$$

$$(P < 0.0001, R^2 = 6.3\%); \text{and}$$

$$\text{Predicted } Log_{10} \text{ WEC} = 1.679 + 0.059 * SR$$

$$(P < 0.0001, R^2 = 11.7\%)$$

The overall effects of year and sheep class remained highly significant ($P < 0.0001$) accounting for 0.58 and 0.42% of SSQ, respectively. The effect of year was due largely to significantly lower LogWEC in 2003 than the other years, while the effect of class was due to hoggets having significantly higher WEC than ewes and lambs in this dataset. There was however a significant interaction between the effects of sheep class and year ($P < 0.0001$, 1.86% of SSQ) such that this effect of higher WEC in hoggets was only evident in 2001 and 2002.

The overall effects of T_{MAX} ($P = 0.04$, 0.05% of SSQ) and EVAP ($P = 0.01$, 0.05% of SSQ) but not T_{MIN} and RAIN on LogWEC were significant. For both T_{MAX} and EVAP the association was positive.

Among the many significant first-order interactions it was notable that the climatic variables T_{MAX} and EVAP had differential effects on sheep class with effects seen largely in ewes only (T_{MAX} * Class $P < 0.0001$, 0.58% of SSQ; EVAP * Class $P < 0.0001$, 1.05% of SSQ). No other significant interactions accounted for more than 0.7% of SSQ.

Discussion

Overall, the results indicate that tactical worm control based on routine monitoring of WEC provided adequate control of worms on all three farmlets for much of the experimental period. However, this approach failed to prevent significant spikes in WEC to values associated with significant production loss on multiple occasions, and ewe mortality up to 5% on one occasion in December 2004, on farmlets A and B. Farmlet C clearly exhibited improved worm control relative to the other farmlets, as evidenced by both lower overall WEC values and fewer anthelmintic treatments required. However, this management system, as implemented, was associated with reduced individual animal productivity overall (Hinch *et al*. 2013*a*, 2013*b*) and by 2005, a SR some 10% lower than the typical farmlet B. The most important factors affecting WEC in the experiment were the time since the last anthelmintic treatment, and the anthelmintic used at that treatment. The magnitude of these effects dwarfed those climatic and management factors that might be expected to influence the epidemiology of gastrointestinal nematode infections via environmental or host-mediated mechanisms. Management factors associated with SR and GP, and climatic indicators of both temperature and moisture availability had significant effects on WEC, confirming that these factors are nevertheless still important.

The main objective of the study was to test whether, compared with typical management (farmlet B), internal parasites can be more effectively managed with improved nutrition (farmlet A) or by IRG (farmlet C). In spite of farmlet A supporting over time a higher SR than farmlet B (48% higher by 2005), there were few differences between farmlets A and B in WEC or the number of drenches applied. The only difference in LogWEC was in 2002 when farmlet A had significantly lower values than farmlet B. On the other hand, slightly more anthelmintic treatments per year were used on farmlet A (4.7) than farmlet B (4.3) although the difference was not statistically significant. The large peaks of WEC in late spring and summer of November and December 2004 on farmlets A and B were both associated with losses of ewes with lambs with acute haemonchosis (4.7 and 5% of ewes on each of these farmlets, respectively). These results suggest that, while intensification of sheep grazing systems in the Northern Tablelands region is unlikely to provide substantial benefits in parasite control, nevertheless the higher levels of green digestible herbage provided by farmlet A (Shakhane *et al*. 2013) enabled a substantially higher SR to be supported without incurring higher worm burdens than on farmlet B. On the other hand, farmlet C had significantly lower WEC and

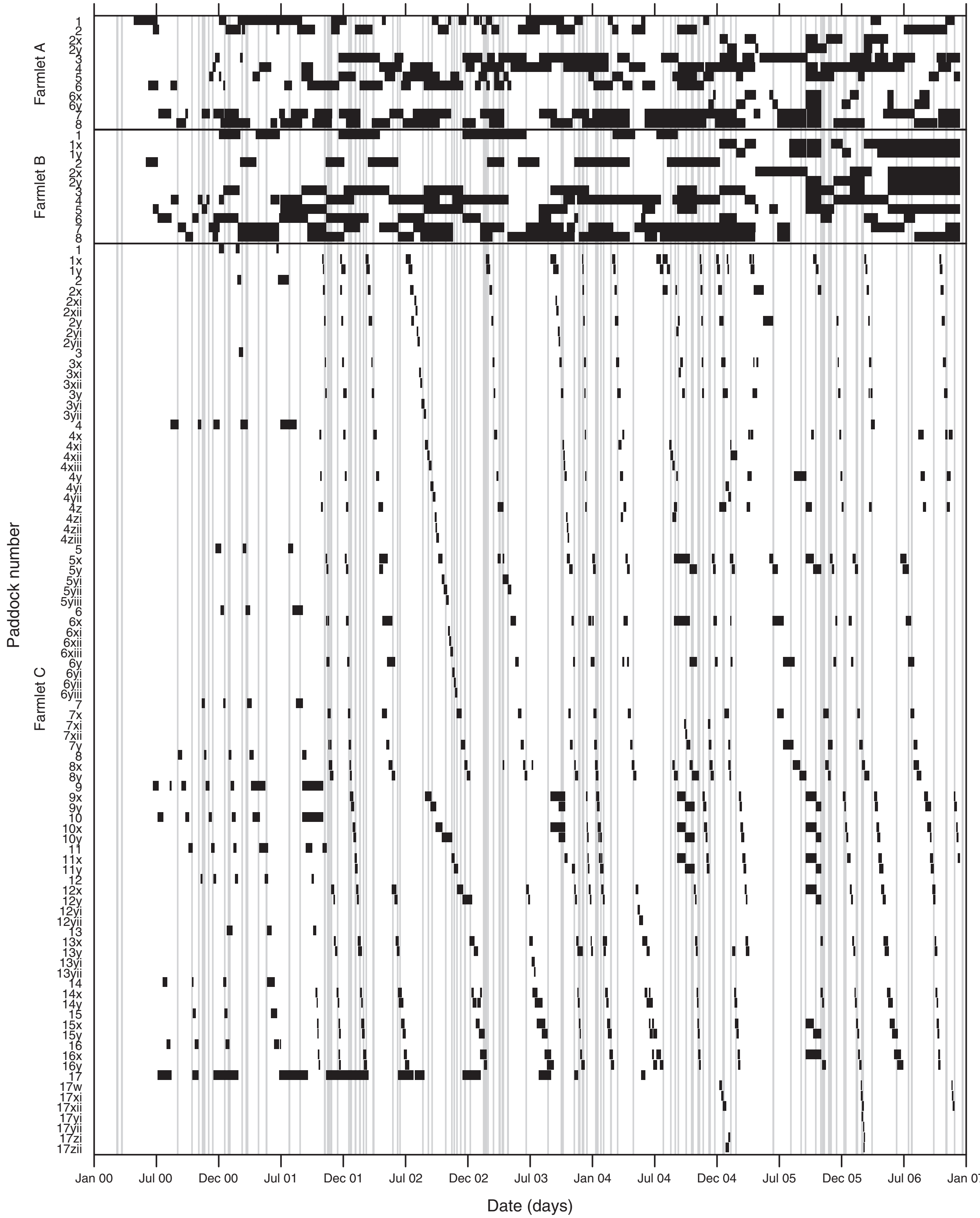

Fig. 6. Daily pattern of grazing practised on each farmlet (*a*: eight major paddocks + two subpaddocks; *b*: eight major paddocks + two subpaddocks; *c*: 17 major paddocks + 41 subpaddock cells). The black bars show grazing periods while the white zones indicate rest periods. The continuous grey vertical lines indicate those days when 10 mm or more rain was recorded [adapted from Scott *et al*. (2013*a*)].

significantly fewer anthelmintic treatments per year than both of the other farmlets. Importantly, these effects were greatest when WEC and anthelmintic treatment numbers were highest, between 2003 and 2005, and this farmlet also did not have the haemonchosis-associated mortality observed in December 2004 on the other two farmlets. Working with a subset of the data from the present experiment, Colvin *et al*. (2008) also reported this beneficial effect of IRG on worm control and in a later report (Colvin *et al*. 2012) showed that the effect of IRG was mediated by reduced larval challenge on pastures rather than improved host resistance to nematode infection. Indeed sheep in the IRG treatment exhibited increased susceptibility to larval challenge in that study.

In the present study, the efficacy of IRG on farmlet C was associated with a shift in the relative abundance of the different parasite genera. As the experiment progressed (years 2002–06) there was a reduction in the proportion of *Haemonchus* in the larval cultures on farmlet C relative to farmlet B of 20.3% units (range 12.6–29.4% units), an increase in the proportion of *Trichostrongylus* by 10.6% units (range 6.2–17.5% units) and an increase in the proportion of *Teladorsagia* by 8.9% units (range 4.1–12.0% units). The *Haemonchus* and *Teladorsagia* larvae identified were almost certainly of the species *H. contortus* and *T. circumcincta*, while the *Trichostrongylus* larvae were most likely *T. colubriformis*, given the predominance of this species of *Trichostrongylus* in the region (Bailey *et al*. 2009*b*).

The reasons why IRG on farmlet C produced this profound effect on WEC and the worm species involved almost certainly relate to its impacts on the free-living ecology of the three main worm species involved. These are likely to operate in three distinct ways as summarised below, with detailed discussion of each following. First, the short grazing periods in the IRG treatments would have largely prevented infection from the current grazing cycle as sheep would have moved to a new paddock by the time significant numbers of infective L_3 larvae would have appeared on pasture. Second, the long rest periods between grazings would have ensured significant die-off of infective L_3 on pasture before the next grazing. Third, spatial and temporal aggregation of fresh sheep faeces in limited parts of the grazed area on farmlet C ensured that, when rainfall events occurred, which were permissive for development of eggs to L_3, only limited parts of the landscape became infective in comparison to farmlets A and B.

On the first of these points, the graze periods on farmlet C were typically less than 5–10 days (Hinch *et al*. 2013*a*; Scott *et al*. 2013*a*) and tended to be longer in winter and shorter in summer. Under optimal conditions of temperature and moisture, first development of *T. colubriformis* and *H. contortus* eggs to the infective L_3 stage in faeces takes 3 and 4 days, respectively (Hsu and Levine 1977) with appearance on herbage at Days 5 and 6, respectively (Cheah and Rajamanickam 1997). The timing of this development is strongly temperature-dependent. At 10°C, the minimum development time of *H. contortus* to L_3 was ~16 days, and thereafter decreased as temperature increased, ranging from 6.4 days at 20°C, 3.5 days at 30°C, and 2.5 days at 37°C (Smith 1990). Based on these data, it is clear that under the IRG system used on farmlet C, little infection of sheep will occur during a given grazing period due to appearance of L_3 on pasture from eggs deposited during that period. Larvae will generally need to survive until the next grazing period to infect a host.

On the second point relating to larval die-off between grazing periods, the factors affecting survival of L_3 on pasture have been reviewed by O'Connor *et al*. (2006). The ensheathed infective L_3 is the stage of the lifecycle most resistant to adverse environmental influences but, as the L_3 cannot feed, survival is reduced by factors that increase motility or metabolic rate, and thus deplete metabolic reserves, such as rainfall and elevated temperatures. Thus, under tropical conditions in Fiji, complete depletion of L_3 on herbage within 5–13 weeks has been reported for *H. contortus* and *T. colubriformis* (Banks *et al*. 1990). Based on these findings, timed, IRG systems that effectively control worms in goats and sheep in the tropics have been devised and successfully implemented (Barger *et al*. 1994; Gray *et al*. 2000).

On the other hand, L_3 are comparatively resistant to the effects of cold, and survive frosts and cold temperatures in the Armidale region that inhibit hatching of eggs to L_3 (Southcott *et al*. 1976; Bailey *et al*. 2009*a*). Larval survival under these conditions is prolonged with Barger *et al*. (1972) predicting L_3 population half-lives of 93 days at 12°C and 85% relative humidity (RH), and only 9 days at 28°C and 35% RH. At 20°C and 65% RH, the half-life was estimated at 33 days. The longer survival period under temperate conditions, coupled with use of rotational grazing schemes that fail to adequately disrupt the nematode lifecycle has resulted in many studies failing to show major benefits of rotational grazing for worm control in sheep in temperate climates (Morgan 1933; Morgan and Oldham 1934; Roe *et al*. 1959*a*; Gibson and Everett 1968). Other studies that did show beneficial effects used such long spelling periods that pasture and animal productivity were impaired (Robertson and Fraser 1933; Eysker *et al*. 2005) as also occurred on farmlet C in this experiment.

Long-term average maximum temperatures for summer, autumn, winter and spring in Armidale are 25.7, 20.1, 13.7 and 20.8°C, respectively. Based on these data and a RH of 50%, the model of Barger *et al*. (1972) would predict half-lives of L_3 on pasture of 15.5, 20, 27 and 19.5 days, respectively. Thus, to reduce L_3 numbers to 10% of their original value would require spelling times of 49, 64, 88 and 62 days, respectively. On farmlet C, rest periods were rarely below 50 days and sometimes over 150 days, with a mean of 98 days (Table 3) thus allowing time for significant larval die-off in most cases. It should be noted that, in practice, these spelling times will overestimate the decrease in larval populations on pasture as L_3 may continue to develop and appear on pasture for several weeks following removal of stock, particularly in the case of *T. colubriformis* and *T. circumcincta* (O'Connor *et al*. 2006). The improved level of control of worms on farmlet C was associated with significantly increased susceptibility to worm infection (Colvin *et al*. 2012) and reduced animal productivity as shown by reduced liveweights (Hinch *et al*. 2013*a*) and fat scores (Hinch *et al*. 2013*b*) of livestock on this farmlet relative to those on farmlets A and B. The long rest periods and lower levels of soil fertility on farmlet C were found to be associated with lower levels of both legume and pasture digestibility within this farmlet (Shakhane *et al*. 2013) and these are likely to have contributed to the reduced productivity.

The third, related reason why the IRG used in farmlet C produced such marked worm control is likely to be spatial and temporal aggregation of faecal deposition such that when rainfall events occurred that were permissive for development of eggs to L_3, only limited parts of the landscape became infective. This can be visualised in Fig. 6 by selecting a single date and running a perpendicular line down through all the paddocks in all three farmlets to represent it. If rainfall falls on that date, where the line passes through black areas (stocked) it will fall on freshly deposited faeces whereas, where it passes through white areas it will fall on unstocked paddocks, mostly not containing fresh faeces. Under dry conditions, rainfall just before or in the first few days after faecal deposition is a requirement for successful development of *H. contortus* and *T. colubriformis* from egg to infective L_3 outside the faecal pellet (Khadijah *et al*. 2013).

Thus on farmlet C, periods of successful development to infective L_3 following rainfall, will be spatially restricted to the small paddocks containing sheep during or shortly before the rainfall event. Over much of the farmlet C landscape, rainfall will have no beneficial effect on larval development because there are no fresh faeces available. In ‘hot spots’ where development occurs, the L_3 that do develop have to survive the long spell period before being exposed to sheep again. This is not the case on farmlets A and B, where rainfall at any time will fall on fresh faeces on a larger proportion of the landscape facilitating development to L_3, which will often be able to infect sheep immediately on emergence from the pasture.

At the start of the farmlet experiment, the dominant nematode genus present was *Trichostrongylus*. On farmlets A and particularly B, there was a rapid decline in the percentage of *Trichostrongylus* from ~75% to less than 10% between 2000 and 2003, after which is remained at comparatively low levels. Most of the decline was associated with a large increase in the proportion *Haemonchus* over the same period. This shift probably reflects the greater reproductive potential of *H. contortus* under the experimental conditions early in the experiment. On farmlet C the situation differed markedly with less ‘displacement’ of *Trichostrongylus* by *Haemonchus* over time, such that there were lower proportions of *Haemonchus* and higher proportions of *Trichostrongylus* and *Teladorsagia* on this farmlet than the other farmlets for most of the period 2002–06. In the broadest terms *Haemonchus* appeared to have been most successful on farmlet B, *Trichostrongylus* on farmlet A and *Teladorsagia* on farmlet C. The lower proportion of *Haemonchus* seen on farmlet C probably reflects its greater susceptibility to lifecycle disruption by grazing management. As noted by Colvin *et al*. (2008), it is likely that the rapid rotational grazing system of Barger *et al*. (1994) under tropical conditions was effective against both *H. contortus* and *Trichostrongylus* spp. but that this was unlikely to be the case in the cool, temperate climate of the Northern Tablelands, which is more conducive to the survival and development of *Trichostrongylus* spp. eggs and larvae between grazing events (Anderson *et al*. 1966; Waller and Donald 1970; Levine and Andersen 1973; Levine *et al*. 1974). On the other hand, the susceptibility of *H. contortus* eggs to desiccation and low temperatures is likely to make them just as susceptible to rapid rotational grazing as they would be under tropical conditions, but probably for different reasons. Temperature and moisture are often limiting in the Northern Tablelands for development of *H. contortus* eggs to L_3 (O’Connor *et al*. 2006, 2007), and failure of development is likely to be a major mechanism operating in this environment. The superior ability of *Trichostrongylus* and *Teladorsagia* species to survive in the embryonated egg stage during cool dry conditions relative to *Haemonchus* could account for the species difference in response to IRG observed in this experiment.

With regard to the objective of investigating sources of variation in WEC during the experiment, it is perhaps not surprising that the majority of the explained variation was due to the last anthelmintic used, and the time since that last anthelmintic treatment. Replacement of generic factors in the model such as season and farmlet with more detailed and proximate measures of environmental and management factors likely to affect WEC failed to explain a great deal more of the observed variation in WEC. On the other hand, they were useful in teasing out the factors that best accounted for the variation. For temperature, a higher proportion of the variation in WEC was explained by including both T_{MIN} and T_{MAX} in the model, than T_{MEAN} or GDD. For moisture, inclusion of both RAIN and EVAP in the model provided a considerably better fit than the inclusion of the derived variables P/E or with ASW providing an intermediate fit. Replacement of the effect of farmlet with both SR and GP resulted in a higher model R^2 whereas the inclusion of either alone did not. In both cases there was a significant positive linear association between SR and GP on LogWEC.

Regarding the objective of investigating the efficacy of anthelmintic treatments during the experiment, the tactical approach used, based upon routine WEC monitoring, provided reasonable control of worms on all three farmlets for much of the experimental period. However, this approach failed to prevent significant spikes in WEC to values associated with significant production loss on multiple occasions, and mortality on limited occasions, particularly on farmlets A and B. As the results of monitoring showed increasing WEC numbers later in the experiment, the Cicerone Management Board recognised that the experimental guidelines laid down for farmlets A and B – of eight paddocks and a minimum of five mobs on each farmlet – were overly constraining in terms of flexible grazing options. Thus, a decision was taken late in the trial to increase the number of paddocks on each of these farmlets to 10, and to increase the paddock number on farmlet C to 40, however these changes were implemented too late to observe the effect of such changes.

When *Haemonchus* is the dominant parasite, effects are likely to be minimal at WEC below 1000, with significant production losses likely between 1000 and 5000, clinical signs and severe production losses between 5 and 10 000 and deaths can be expected in the range 10–30 000 (Brightling 1994). When *Haemonchus* is not present, the respective values are <200, 200–500, 500–2000 and >2000. The *Haemonchus* values are consistent with the WEC-associated mortality observed on farmlets A and B in December 2004. To prevent such spikes, the frequency of WEC sampling during the high-risk months in late spring and summer may need to be increased, and more sophisticated treatment thresholds adopted. Adoption of a tactical integrated parasite management program based on routine WEC monitoring has been shown in other studies to reduce the adverse impact of worms and frequency of anthelmintic treatment (Kelly *et al*. 2010) and such an IPM approach is central to the recommendations of WormBoss, Australia's national sheep worm control program (http://www.wormboss.com.au/, accessed 1 April 2013). Adoption of the WormBoss summer rainfall IPM program could be expected to reduce the likelihood of the spikes in WEC observed in this experiment.

The overall frequency of anthelmintic treatment of four per annum in the present experiment (Table 3) is well above those reported for the Northern Tablelands region in the IPM 2004 Benchmarking Survey (Reeve and Thompson 2005). In that study the 161 respondents from that region reported a mean treatment frequency of 3.1 in adult ewes in 2003, compared with mean values of 6, 5 and 4 in that year for farmlets A, B and C. This is likely due to the significant numbers of quarantine drenches used on the experiment (two per year for ewes and one per year for other sheep), the tactical approach used in the study, with intensive WEC monitoring taking place, and also the predominant use of short- rather than long-acting anthelmintics. The FECRT conducted on farmlet C in 2003 showed that there was evidence of resistance to ivermectin and albendazole but neither was used alone after this point. There was evidence of resistance to closantel based on a reduced duration of protection, and this anthelmintic was also not used alone after 2002.

In conclusion, the results show that, in a summer rainfall temperate environment with *H. contortus* as the dominant parasite, improved host nutrition in a higher input system (farmlet A) did not provide more effective control of gastrointestinal nematodes than typical management (farmlet B); however, it was observed that gastrointestinal nematode control was no worse on farmlet A than on farmlet B in spite of farmlet A supporting a 48% higher SR by later in the trial period (2005). The experiment provided strong support for the proposition that IRG (farmlet C) does provide more effective control of gastrointestinal nematodes as evidenced by significantly lower WEC counts and anthelmintic treatment frequency. As reported elsewhere (Colvin *et al*. 2012) this effect is mediated by reduced larval challenge on pasture, rather than improved host resistance. Indeed host resistance to worms was lower on farmlet C due to reduced exposure. Tactical worm control based on routine monitoring of WEC provided adequate control of worms on all three farmlets for much of the experimental period but failed to prevent significant spikes in WEC to values associated with significant production loss on multiple occasions, and mortality on limited occasions, particularly on farmlets A and B.

The most important factors affecting WEC in the experiment were the time since the last anthelmintic treatment, and the anthelmintic used at that treatment. The magnitude of these effects dwarfed those climatic and management factors that might be expected to influence the epidemiology of gastrointestinal nematode infections via environmental or host-mediated mechanisms.

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