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Population dynamics and production effects of sheep lice (*Bovicola ovis* Schrank) in extensively grazed flocks

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Abstract. An experiment was conducted to characterise population dynamics of lice and associated production loss in extensively grazed flocks infested at different times after shearing. Merino wethers were allocated to six groups of 31 sheep. In the first year (Y1), one sheep in each of two groups was infested with 2500 lice at 6 weeks after shearing (September), sheep in two groups were infested at 4 months (December) and two groups remained uninfested. In year 2 (Y2), infestations carried over from Y1, but a lousy sheep was added to each 6-week infestation mob. In year 3 (Y3), the infested mobs were treated and remained lice free, while lousy donor sheep were added to the two previously uninfested mobs. In Y1, lice appeared to die out in one 6-week-infestation group and were found on only two sheep before next shearing in the other. Lice persisted and spread in the two 4-month-infestation flocks, reaching mean counts (±s.e.) of 0.5 (±0.2) and 0.2 (±0.1) per part before shearing. In Y2 and Y3, lice persisted and increased in all infested flocks, reaching mean counts of 2.3 (±0.6), 8.5 (±1.5), 3.6 (±0.6) and 2.8 (±0.7) per part in Y2 and 1.0 (±0.2) and 1.2 (±0.4) per part in Y3. The count of 8.5 was in the flock with both a carry-over infestation and an infestor sheep. Exponential and logistic models were fitted to describe lice increase; differences in fleece derangement reflected louse numbers. Clean fleece weight was higher in flocks without lice in all years (0.12 kg/head in Y1; 0.22 kg/head in Y2 and Y3; $P < 0.05$). Classer-assigned colour scores (although not measured colour), cott score and line into which the wool was classed also differed significantly ($P < 0.05$) between infested and non-infested flocks and there was an indication that staple length was reduced in more heavily infested flocks. In spring-shorn flocks in environments with high solar radiation and no lice present at shearing, even if lice subsequently enter the mob, it appears unlikely that they will increase to levels where serious economic loss will be experienced before next shearing. The study also indicated that lice could persist in flocks at levels unlikely to be detected by most commercial wool producers for extended periods, possibly through one season, which may help to explain reports of new infestations with no apparent source.

Introduction

Sheep lice are one of the three most economically important health issues for sheep production in Australia (Sackett *et al*. 2006). Historically, lice have been controlled mainly with the use of chemical lousicides, often applied as routine annual treatments after shearing, regardless of whether or not lice are detected. In recent years, with increased sensitivity to chemical residues in wool markets and society generally (Savage 1998; Russell 2001), the development of resistance to widely used chemicals (Levot 1995; James *et al*. 2008) and ongoing cost of production pressures, there has been an increased focus on the use of integrated programs and more insecticide-rational approaches to lice control (James 2002, 2010; Walkden-Brown *et al*. 2006; Horton *et al*. 2009).

One of the central tenets of integrated pest management (IPM) is the application of therapeutic treatments with regard to economic thresholds, or use only when the economic benefits expected will exceed the cost of treatment. For post-shearing treatments, most advisory recommendations state that all sheep should be treated if any lice are detected, regardless of the level of infestation. This is the best course of action in most circumstances, because in Australia the registration of ovine lousicides for post-shearing treatment requires that they will reduce lice to non-detectable levels if applied according to label directions (Australian Pesticides and Veterinary Medicines Authority, Guideline 23) and it is a general expectation that a well applied post-shearing treatment will eradicate lice if all animals are treated. With long wool

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treatments (treatments applied more than 6 weeks after shearing) eradication is not expected and, theoretically, the concept of economic thresholds is applicable.

However, the development of such thresholds requires knowledge of the likely rate of lice increase and associated production loss if sheep are not treated. Most previous data on economic losses from lice have been derived from experiments in which all or most sheep in the mob began the year infested with lice (e.g. Wilkinson *et al*. 1982). This is not the case in most commercial situations where infestations generally begin from one or a few lousy sheep and then spread through the mob. In the two previous studies of economic effects where infestations started from lousy sheep introduced to the mob, one mob with 8 months wool (Cleland *et al*. 1989) and one with 9 months wool (Elliott *et al*. 1986), there was no measurable reduction in wool cuts or value at the next shearing and a long wool treatment would have had little economic benefit. Information was needed to assess the likely rate of lice population build-up and associated economic loss when mobs initially became infested from one or a few lousy sheep early in the wool-growing cycle, rather than in the last 6 months, as in the two studies noted above.

In the present paper, we describe investigations of the dynamics of lice populations and their effects on fleece derangement and production loss in flocks that were infested from one or a few infested sheep soon after shearing, with a view to the development of economic thresholds for long wool treatments.

Materials and methods

Environment

The experiment was conducted at Rosebank Research Station at Longreach in Queensland, Australia. Longreach has an average annual rainfall of 435 mm and mean winter and summer maximum (minimum) temperatures of 24.4°C (7.9°C) and 36.7°C (22.6°C), respectively. The annual rainfall totals for the 3 years of the study were 351 mm, 381 mm and 562 mm. Sheep grazed on native Mitchell grass-dominant pastures throughout the study.

Experimental animals

In total, 378 Merino wether hoggets were fleece-weighed and mid-side sampled at shearing in August, before the start of the study. Sheep were ranked on the basis of greasy fleece weight at shearing and 186 sheep from the centre of the greasy fleece weight distribution were selected for the study. Sheep within groups of six ranked on fleece weight were then randomly allocated to six treatment groups balanced for fleece weight (Table 1). They were identified with different-coloured tags according to the group, so that any straying sheep could be readily detected, and the groups were randomly allocated to paddocks of 50 ha in area.

The design was initially a random block, with three treatments and two replicates for each treatment. The three treatments in Year 1 (Y1) were as follows: infested at 6 weeks after shearing, in late September (S1 and S2), infested at 4 months after shearing, in December (F1 and F2) and not infested (C1 and C2). In Year 2 (Y2), the same four groups remained infested and the other two groups remained lice free. For Year 3 (Y3), a crossover design for louse infestation was used, with the four previously infested groups treated with a double dose of a commercial triflumuron backliner (Zapp, Bayer Australia Ltd, Pymble, NSW) after shearing and kept louse free whereas lousy donor sheep were added to the two previously uninfested groups. Sheep remained in the same paddock throughout the 3 years of the study and in all years sheep in the louse-free treatments were treated with double-dose backliner to reduce the possibility of inadvertent infestation. Flocks were managed according to the Australian Model Code of Practice for the Welfare of Animals under Department of Primary Industry and Fisheries Animal Ethics Committee approvals SA2005/11/72 and SA2006/02/91.

Infestation

In Y1, one sheep from each of the two 6-week mobs (S1 and S2) and the two 4-month groups (F1 and F2) was artificially infested with 2500 lice (*Bovicola ovis*), which equates to a count of approximately one louse per part (James and Moon 1999). For each infestation, 5000 lice were collected from sheep from a recently purchased lousy group and counted into 10 vials of 250 lice each. Lice were not characterised for resistance status because this was not considered relevant to the experiment. On the day of infestation, a sheep was chosen randomly from each group to be infested and 250 lice were emptied into the fleece at five sites on each flank.

In Y2 in the infested groups, infestations were allowed to carry over from Y1 after shearing. However, because louse numbers were low or possibly zero in the S1 and S2 groups, a lousy infestor sheep with a mean louse count of two lice per part was added to each of these two groups after shearing.

In Y3, one sheep with a louse count of two lice per part was added to each of the two infested groups immediately after shearing in September. However, lice populations on these donor sheep decreased to non-detectable levels over summer

Table 1. Mean (s.e.) for production characters for experimental groups at the commencement of the study

Group	Treatment in Year 1	Bodyweight (kg)	Greasy fleece weight (kg)	Clean fleece weight (kg)	Fibre diameter (μm)
S1	Infested 6 weeks after shearing	40.93 (0.85)	3.80 (0.03)	2.57 (0.05)	20.41 (0.23)
S2	Infested 6 weeks after shearing	40.50 (0.83)	3.78 (0.03)	2.52 (0.05)	20.70 (0.26)
F1	Infested 4 months after shearing	41.78 (0.75)	3.77 (0.03)	2.53 (0.05)	20.36 (0.20)
F2	Infested 4 months after shearing	40.51 (0.83)	3.78 (0.03)	2.60 (0.05)	20.35 (0.28)
C1	Not infested	40.39 (0.65)	3.78 (0.03)	2.61 (0.05)	20.08 (0.25)
C2	Not infested	40.99 (0.72)	3.78 (0.04)	2.57 (0.04)	20.24 (0.28)

and two replacement infestor sheep with counts of about two lice per part were added to each group on 20 March.

Assessment of louse numbers and scoring for fleece derangement

At 2–3-month intervals, sheep were mustered in their groups, inspected for lice and scored for fleece derangement. Inspection for lice was carried out in an elevated race and the number of adult and nymphal lice counted in 24 10-cm wool parts disposed in three lines of four along each side of each sheep (James *et al*. 2002). Because the sheep that were artificially infested in Y1 were part of the originally allocated sheep, these were included in all analyses. However, none of the animals added to the experimental groups as louse donors was included in analyses of either louse counts or production characters.

Fleece derangement, often used as an indicator of the presence of lice, was assessed by determining a wool rub score from 0 (no derangement) to 6 (grossly matted fleece, often with areas rubbed bare), according to the method of James *et al*. (2007), with reference to photographic standards. Scoring was done independently by observers on each side of the race and an average score for the two sides was calculated for each sheep for analysis.

Production measures

Sheep were weighed and shorn in August, at the commencement of the study, then at shearing in August in Y1, in September in Y2 and at the start of October in Y3. Sheep were also weighed at each inspection for lice and fleece weights and mid-side wool samples were collected at each shearing. Table 2 provides a summary of the production characters assessed on the experimental sheep in each year. Fleece-sample measurements were carried out by commercial wool-testing laboratories. Fleece yield, fibre diameter and associated fibre-diameter parameters, fibre curvature and length and strength were measured by Australian Fibre Testing, Morven, Queensland, and objective colour (yellowness) was measured by Australian Wool Testing Authority Ltd, Melbourne, Victoria. The wool classer assigned scores for colour at shearing (1 = normal, 2 = some yellowing, 3 = marked yellowing) and cott (1 = normal, 2 = soft/medium cott, 3 = hard cott) in Y2 and Y3 and the fleece line into which each fleece was classed was recorded.

Table 2. Production characters measured (+) in the study and years in which they were assessed

Character	Year assessed			
	Start of study	Year 1	Year 2	Year 3
Bodyweight (kg)	+	+	+	+
Greasy fleece weight (kg)	+	+	+	+
Clean fleece weight (kg)	+	+	+	+
Yield (%)	+	+	+	+
Fibre diameter (μm)	+	+	+	+
Coefficient of variation of fibre diameter (%)	+	+	+	+
Fibre curvature (°/mm)	+	+	+	+
Staple length (cm)			+	+
Coefficient of variation of staple length (%)			+	+
Stable strength (N/ktex)			+	+
Classer colour score			+	+
Classer cott score			+	+
Fleece line			+	+
Objective colour (Y–Z)				+

Analysis

For Y1, non-categorical data were analysed as a one-way analysis of variance, with group as the experimental unit and three treatments with two replicates each. For Y2 and Y3, groups were classified as infested or not infested, with two replicates not infested and four infested in Y2 and two infested and four not infested in Y3. The data were analysed both within years and over Y2 and Y3 as a cross-over design. Because the groups remained in the same paddocks throughout the study, any nutritional differences in paddocks are included in the group effect.

For analysis of bodyweight change in the different groups, linear regressions were fitted to weights over time for individual animals. This method was considered to give the best estimate of liveweight change within a year because all weights contributed. The slopes estimated from individual sheep regressions were analysed by analysis of variance, with the group as the experimental unit, as for the other parameters.

For the categorical data (classer colour score, cott score and wool line), a generalised linear model with a binomial error distribution and a logit link function was fitted to the number of sheep in a group with a certain classification out of the total number of sheep in that group. As the classer had scored some fleeces as '1 to 2', or '2 to 3', which were coded as 1.5 or 2.5, the data were reclassified into the following categories: 1 = <1.1, 2 = >1.1 but <2.1 and 3 = >2.1, and these scores were analysed. The data were analysed both within Y2 and Y3 and as a cross-over design.

Exponential and logistic models were fitted to the data for lice build-up in the different mobs because these made most biological sense and fitted the data well in most cases. Regressions of lice numbers on week were generally highly significant ($P < 0.05$) with both models and as prediction of lice numbers gave similar results in most instances, only the one that explained the most variance for each mob is presented here. All analyses were conducted using GENSTAT v10 (Payne *et al*. 2007).

Results

Louse numbers

In Y1, louse numbers remained at low levels, particularly in the groups infested at 6 weeks after shearing. At the first inspection, 92 days after the application of lice in the 6-week infestation groups, only one louse could be found on each of the two infestor sheep and no lice were found on any of the other sheep in these two groups. No lice were found after this time on any sheep in the first replicate (S1) (5 inspections) and no lice were found in the second replicate (S2) until the penultimate count before shearing. At this count, two lice were found on the initially infested sheep and at the final count lice were again found on the infestor sheep (2 lice) as well as on another sheep in the group (4 lice).

In those sheep infested at 4 months (Day 128), 17 lice were found on the infestor sheep in Group F1 at the initial inspection 9 weeks later and lice numbers continued to build on this sheep until shearing. However, only three lice were found on the infestor sheep in replicate F2 at the first inspection and no lice were detected on this sheep again until the last count before shearing. Lice were also not found on other sheep in group F2 at the next two inspections, but lice were found on three sheep at the penultimate count before shearing (35 weeks after initial infestation). At the final count before shearing in Y1, 83% of sheep in Group F1 had lice detected and the mean count was 0.49 (±0.19) per part. In group F2, 23% of sheep had lice detected and the mean count was 0.19 (±0.13) per part.

In Y2, in the mobs where infestations came only from carry over populations, at the first inspection 8 weeks after shearing, lice were found on just one sheep in Group F1 and on none in Group F2. However, lice were found on sheep in both groups at the next inspection and populations continued to increase after this time. At the last count before shearing in Year 2, both groups had moderate louse levels (mean ± s.e.: 3.6 ± 0.59 and 2.8 ± 0.64 per part for groups F1 and F2, respectively) and all but one sheep in these two groups had lice detected.

Counts on the two donor sheep added to Groups S1 and S2 dropped from an average of two lice per part at introduction to undetectable levels at 16 weeks (February). However, lice had spread to other sheep in the mob and the populations in these two groups continued to build until Year 2 shearing (Fig. 1). At the final count before shearing, all sheep in these two groups were infested and the mean count per part had reached 2.4 ± 0.61 per part in Group S1 and 8.5 ± 1.5 per part in Group S2.

In Y3, there was also a decline in louse counts on the infestor sheep over the summer. In group C2, no lice were found on the infestor sheep at the first inspection in December (14 weeks after the introduction). In group C1, although lice were found at both the December and February inspections, by the time of the next inspection in April (23 weeks after the introduction), lice numbers had dropped to undetectable levels. Because lice were found on only one other sheep in each group at the February inspection and the lice numbers had fallen to very low levels on the infestor sheep, to ensure a louse challenge, additional infested animals were added in March as described above. Louse counts increased in the challenged groups after this time, and before shearing, lice were detected on 93% of sheep in Group C1 and on 97% in Group C2, with final

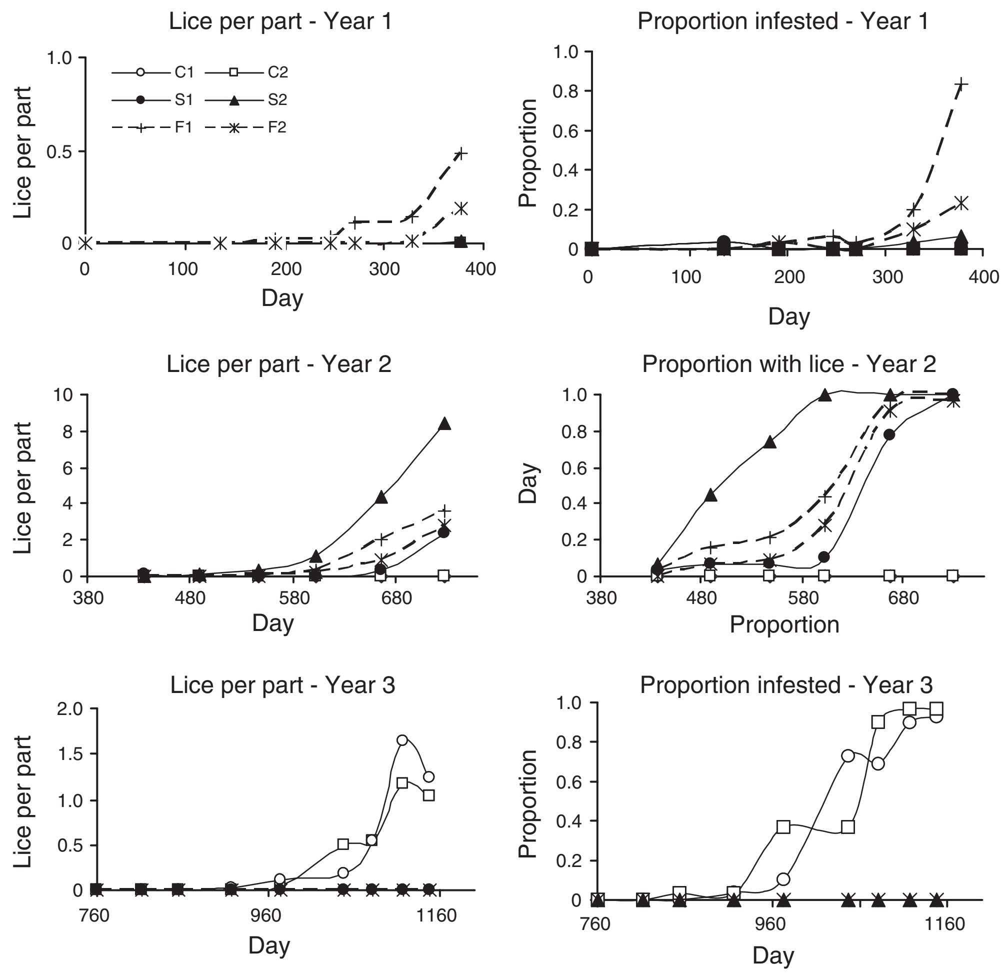

Fig. 1. Increase in louse numbers and proportion of sheep in the mob on which lice were detected in the six experimental groups in the 3 years of the study. The *y*-axis intersects with the *x*-axis at shearing in each year.

louse densities of 1.04 ± 0.19 and 1.24 ± 0.36 per part, respectively. The louse densities recorded at the penultimate count 1 month earlier were slightly higher at 1.18 ± 0.20 per part and 1.64 ± 0.35 per part, respectively, but these differences were not significant.

In Y1 and Y2, no lice were detected at any inspection of sheep in Groups C1 and C2. In Y3, the double dose of triflumuron was effective in eradicating lice and no lice were detected in the four previously infested groups.

The best-fitting equations describing the pattern of increase in mean louse count per part within mobs in each year are shown in Table 3 and explained a high proportion of variation in most instances. In Y1, because lice build-up in the F1 mob commenced with infestation at 4 months after shearing, the equation represents build-up only over 8 months and the data were collected when sheep had a significant length of wool present and during a period with a greater proportion of cool weather. In Y2, because there were carry-over infestations in most or possibly all of the infested groups, infestations were potentially already spread among several sheep in the flock at the start of the year, no doubt influencing the rate of population increase observed. In the S1 and S2 groups, infestor sheep were also added, providing a further source of infestation. Because the original donors were added immediately after shearing in Groups C1 and C2 in Y3, the models fitted use the day after shearing as the starting point. However, because lice counts dropped to undetectable levels in one group and to almost undetectable levels in the other before further donors were added at about 6 months after shearing, a later starting date for fitting the model may have been appropriate.

Fleece derangement

The pattern of increase in rub score is shown in Fig. 2 and reflected the build-up in lice numbers (Fig. 1), both across and within years. In Y1, rub score at the last inspection was significantly ($P < 0.05$) higher in the groups infested at 4 months than that in controls, but there were no other significant differences. In Y2, the infested groups had significantly higher rub scores than did controls at the inspection 24 weeks after shearing and at all subsequent inspections, whereas in Y3, the difference between the infested and control groups was significant at 29 weeks after shearing and at all subsequent inspections. However, rub scores were not available for earlier inspections in Y3. Patterns in other measures of wool rub (e.g. proportion of sheep with average rub score of >1 and maximum rub score) reflected that for the mean rub score. There was also a significant correlation between lice numbers and rub score within infested flocks at most inspections, once louse numbers started to build (data not shown).

Production characters

Year 1

Selecting from the centre of the flock distribution for greasy fleece weight formed experimental groups that initially had low variability for the major economic characters bodyweight, greasy and clean fleece weight and fibre diameter (Table 1) and provided maximum opportunity for the production effects of lice to be detected. However, the only character for which there was any significant effect of treatment in Y1 was clean fleece weight, which was lower in the groups infested at 4 months than in the 6-week infestation groups or controls (Table 4). This was the only treatment to have appreciable numbers of lice detected, with final louse counts of 0.49 per part and 0.19 per part and 83% and 23% of sheep with lice detected in the two replicates (Fig. 1). Even though most sheep were infested for only part of the year and louse numbers were low, the level of infestation was sufficient to bring about a statistically significant reduction in clean fleece weight of 0.12 kg per head, in comparison to the controls and 6-week infestation groups.

Years 2 and 3

In Y2 and Y3, when lice numbers were higher than in Y1, the main characters that showed a difference between the infested and uninfested groups ($P < 0.05$) were clean fleece weight and yield (Table 5), classer-assessed colour score (Fig. 3*a*), cott score (Fig. 3*b*) and wool line to which fleeces were assigned (Fig. 3*c*). For clean fleece weight, there was no significant difference within year in Y2 and Y3. However, when analysed in the more sensitive cross-over design, which removed any confounding paddock effects, the clean fleece weight of the groups was found to be significantly lower, with a difference of 0.22 kg per head in favour of the non-infested sheep.

There were also significant differences, or differences that approached significance, for both yield and greasy fleece weight, which contributed to the difference in clean fleece weight. Yields were significantly lower in infested groups in the cross-over analysis for Y2 and Y3 and the difference approached significance ($P = 0.057$) in Y2. The effect on greasy fleece weight was significant in the cross-over analysis, although

Table 3. Best-fit models for increase in lice per part over time in different mobs and years

Year	Group	Best-fit models for increase in lice populations by year and group	Final louse count	%variation accounted for
Y1	F1	Lice/part = $0.0061 + 0.00334 \times (1.395^{week})$	0.49	97.3
Y2	S1	Lice/part = $0.0149 + 0.0000537 \times (1.2332^{week})$	2.37	99.6
Y2	S2	Lice/part = $0.0896 + 10.281/(1 + \exp(-0.2031 \times (week - 43.75)))$	8.45	99.9
Y2	F1	Lice/part = $0.0197 + 3.8266/(1 + \exp(-0.2965 \times (week - 41.688)))$	3.62	99.9
Y2	F2	Lice/part = $-0.00531 + 5.05/(1 + \exp(-0.1861 \times (week - 49.833)))$	2.79	100
Y3	C1	Lice/part = $0.001 + 1.45/(1 + \exp(-0.174 \times (week - 47.7)))$	1.04	81.2
Y3	C2	Lice/part = $0.1033 + 0.8718/(1 + \exp(-1.753 \times (week - 46.36)))$	1.24	93.1

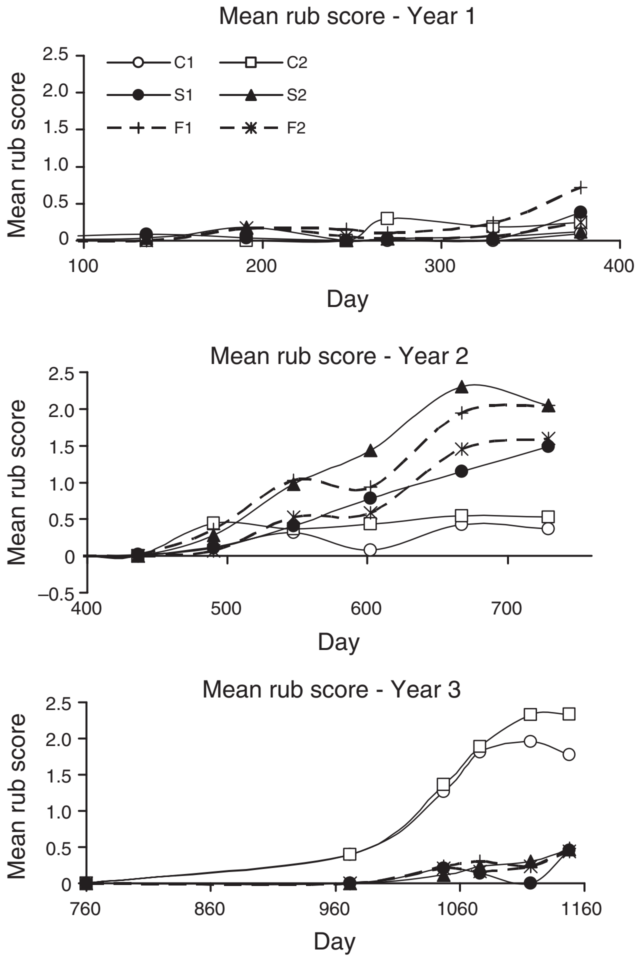

Fig. 2. Increase in fleece derangement with time in different experimental groups in the 3 years of the study.

Table 4. Differences among the three treatment groups in production characters measured in Year 1

Bodyweight change was analysed as the slopes of linear regression fitted over time within year for individual animals. CV, coefficient of variation. Significant levels are presented for comparisons with the not infested group for all instances where $P < 0.1$. n.s., not significant; $P > 0.05$

Character	Not infested	Infestation 6 weeks	Infestation 4 months	Statistical significance
Bodyweight change (kg/day)	0.0437	0.0503	0.0428	n.s.
Greasy fleece weight (kg)	5.72	5.85	5.59	n.s.
Clean fleece weight (kg)	3.98	3.98	3.86	$P = 0.026$
Fibre diameter (μm)	22.1	22.9	22.3	n.s.
CV fibre diameter (%)	19.10	19.30	19.69	n.s.
Yield (%)	69.5	68.1	69.1	n.s.
Fibre curvature (°/mm)	88.9	88.4	90.4	n.s.

Table 5. Differences between non-infested and infested groups in production parameters in Years 2 and 3 and when analysed as a cross-over design

Bodyweight change was analysed as slopes of regression over time within year for individual animals. CV, coefficient of variation. Significant levels are presented for all instances where $P < 0.1$. n.s., not significant; $P > 0.05$

Character	Year	Not infested	Infested	Statistical significance
Bodyweight change (kg/day)	Y2	0.014	0.016	n.s.
	Y3	0.0139	0.0192	n.s.
	Y2 and Y3	0.0138	0.0175	n.s.
Greasy fleece weight (kg)	Y2	4.69	4.75	n.s.
	Y3	5.05	4.78	n.s.
	Y2 and Y3	4.90	4.80	$P = 0.009$
Clean fleece weight (kg)	Y2	3.25	3.03	n.s.
	Y3	3.44	3.22	n.s.
	Y2 and Y3	3.35	3.13	$P < 0.001$
Fibre diameter (μm)	Y2	22.37	22.98	$P = 0.043$
	Y3	22.57	22.46	n.s.
	Y2 and Y3	22.53	22.78	n.s.
CV fibre diameter (%)	Y2	18.60	18.78	n.s.
	Y3	18.64	18.77	n.s.
	Y2 and Y3	18.62	18.78	n.s.
Yield (%)	Y2	69.33	63.68	$P = 0.057$
	Y3	68.02	67.16	n.s.
	Y2 and Y3	68.3	65.04	$P < 0.001$
Fibre curvature (°/mm)	Y2	84.8	85.3	n.s.
	Y3	78.1	74.7	n.s.
	Y2 and Y3	81.8	80.4	n.s.
Length (mm)	Y2	95.22	95.43	n.s.
	Y3	110.7	105.6	$P = 0.043$
	Y2 and Y3	103.4	100.9	n.s.
CV length (%)	Y2	3.14	3.84	n.s.
	Y3	4.31	4.07	n.s.
	Y2 and Y3	1.22	1.29	n.s.
Strength (N/ktex)	Y2	45.22	47.41	n.s.
	Y3	39.55	38.80	n.s.
	Y2 and Y3	42.6	43.3	n.s.
Objective scoured colour	Y3	9.91	9.99	n.s.

the difference was only 0.1 kg per head in favour of the non-infested sheep.

Fibre diameter was significantly different between infested and non-infested groups in Y2, although the difference was small (0.62 μm) and there was no difference in the cross-over analysis. Staple length was significantly lower in the infested group in Y3, although there was no difference in Y2, when lice numbers and rubbing scores were higher, and again no difference in the cross-over analysis.

Classer assessment

Classer's scores for wool colour and cotting were significantly different between groups in most analyses, with a significantly higher proportion of fleeces from the non-infested groups classified as having normal colour and no cotting and significantly higher proportions of infested sheep assessed as having some or marked yellowing or soft/medium and hard cotting. However, despite the significant ($P < 0.001$) difference

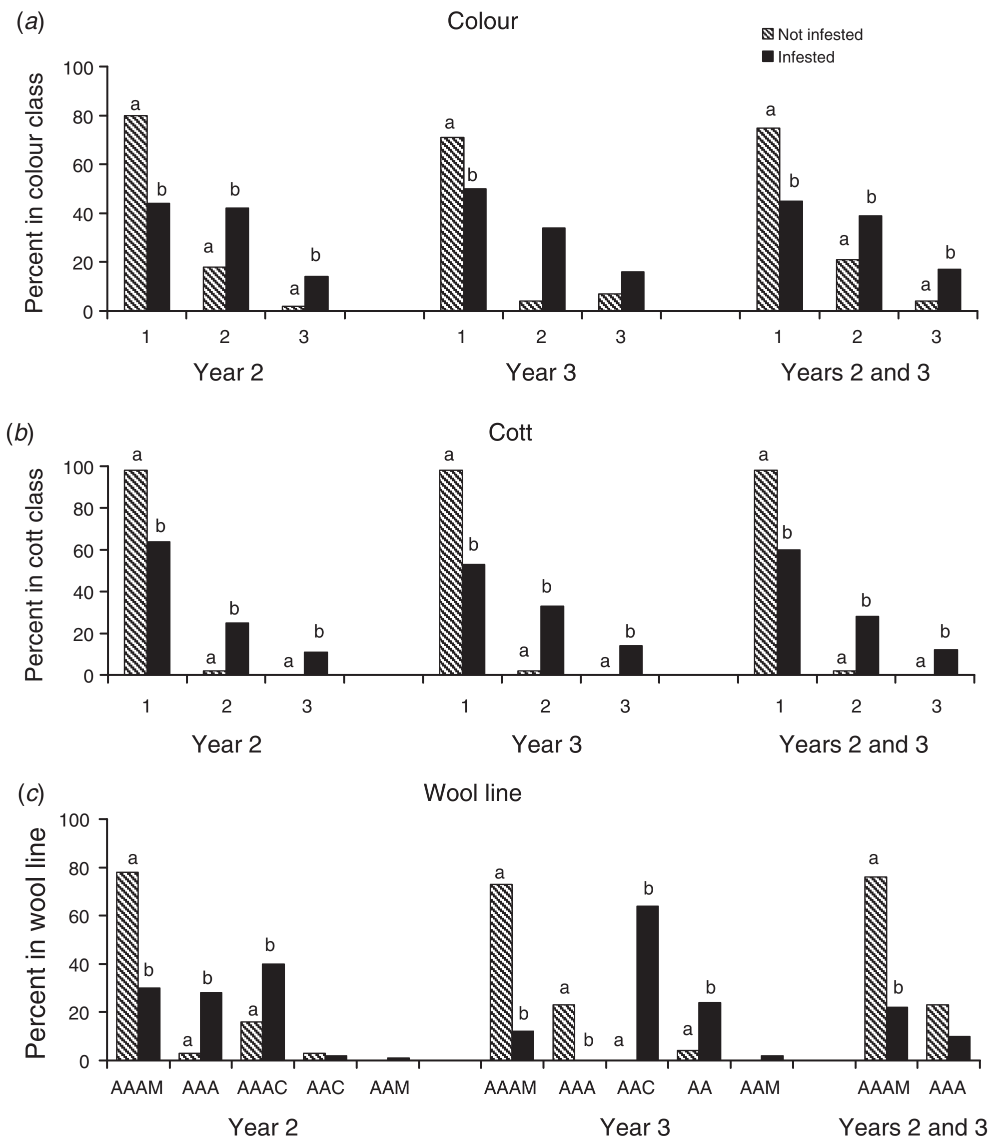

Fig. 3. Differences in proportions of sheep in infested and non-infested groups classified by the wool classer in (*a*) different colour-score groups, (*b*) different cotting-score groups and (*c*) different wool lines at shearing. Percentages with different letters for infested and non-infested groups within a colour class, cott class or wool line and year are significantly ($P < 0.05$) different from each other.

in classer colour scores in Y3, there was no significant effect on measured scoured colour (Table 5).

It appeared that the criteria the classer used to form his lines in Y3 were slightly different from those used in Y2, so that conduct of a cross-over analysis was not possible for some lines. In addition, the criterion used to separate fleeces into the second line (AAA) may have been different in the 2 years, with many sheep from the infested group in this line but few from the uninfested groups in Y2, whereas in Y3 all of the fleeces from this line were from uninfested groups. However, there was a larger proportion of fleeces from infested flocks classed into lower lines within year and the cross-over analysis confirmed a much higher proportion of fleeces from uninfested groups in the top line (Fig. 3*c*).

Discussion

Louse numbers

In the first year of the study, the initial infestations were carried out in late September on sheep with 6 weeks wool growth. Although 2500 lice were applied to each of two sheep, only two lice could be found at the next inspection, 13 weeks later. No lice were subsequently found before the next shearing in Group S1, whereas in Group S2, although no lice were found in this mob at the next three inspections, lice were again detected on the infestor sheep at the penultimate count before Y1 shearing, and on this sheep and one other (total of six lice found) at the last count before shearing. At the final count before shearing in the second year, lice density on the same sheep averaged 1.3 per part, which equates to total lice numbers of more than 3000 (James and Moon 1999). Inspection in the present study was very much more meticulous than would typically be carried out by commercial wool producers and this sheep would have probably remained undetected for at least one season, but carried sufficient lice to commence an infestation when conditions were suitable for lice numbers to increase. It therefore appears that lice may be able to survive in flocks at undetectable levels for an extended period of time and then re-emerge to cause an infestation when conditions are suitable. Such emerging infestations would probably have been attributed to a new introduction rather than a carry-over infestation and may help explain producer reports of new infestations with no identifiable origin.

Lice numbers declined on all sheep over summer in both the shorn sheep and lice donors. However, the decline was most marked on the shorn sheep. The reduction in louse numbers as a result of shearing has been estimated at between 30% and 50% (Murray 1968). However, in Groups F2 and F1 in which 83% and 23% of sheep, respectively, had lice detected before shearing, at the next inspection 8 weeks after shearing, lice were detected only on one sheep in Group F2 and none in F1 and mean louse densities had declined by more than 99%. No doubt this was due to the high levels of incident solar radiation and associated high temperatures to which the lice were exposed over summer in the Longreach environment (Murray 1968). This decline in louse numbers to almost undetectable levels following shearing in flocks known to be infested underlines the difficulty for commercial growers in ensuring lice freedom in purchased sheep and maintaining property biosecurity.

Even where unshorn donor sheep were introduced to the mobs after shearing, lice declined to undetectable levels over summer and there was no substantial increase in louse numbers in the first 6 months after shearing in any of the infested mobs in any year (Fig. 1). However, it is notable that in the study of Niven and Pritchard (1985), conducted in a similar environment in south-western Queensland where sheep were shorn in June and commenced the summer (November) with 4–5 months wool and substantial louse burdens, lice numbers increased steadily through summer. Wilkinson *et al.* (1982) in Western Australia also found that lice increased during summer and suggested that louse build-up was more influenced by wool length than by seasonal conditions. Time of shearing may therefore be an important consideration in designing integrated approaches to the control of lice in areas subject to high levels of solar radiation and temperatures during summer.

It is notable that the heaviest final louse infestations occurred in the infested groups in Y2. In this year, flocks had been infested in the previous season, there had been at least some spread of lice among sheep and there were carry-over infestations in at least three of the four flocks. This contrasts with the situations in Y1 and Y3, where initial infestations began from individual sheep. These results suggest that in spring- or summer-shorn flocks in similar environments, if the mob is free of lice at shearing, it is unlikely that there will be serious economic loss from lice within the first year of infestation, unless the mob is subjected to an exceptionally high louse challenge.

In most instances the models that we provide closely characterised the pattern of build up that occurred in the different flocks. The lower percentage of variation accounted for in the C1 and C2 groups in Y3 may have been due to the use of relatively inexperienced temporary staff to conduct some louse counts in the final year of the study. The equations presented may enable the use of these data for future studies modelling lice population dynamics and economic effects. They may also assist prediction of rates of lice population build up in other situations, although it should be noted that many environmental, management and intrinsic sheep factors can affect the rate of lice increase (Murray 1963, 1968; James 1999).

Fleece derangement

In attempting to develop practically useful economic thresholds for treatment, there must be a suitable means of estimating the level of infestation present in a mob. Directly counting lice is laborious and time-consuming and unlikely to be acceptable to growers. In addition, because a large proportion of sheep in the mob may not have lice, a large sample of sheep will need to be inspected to give an acceptably accurate estimation of the level of infestation present. James *et al.* (2007) concluded that fleece derangement could be a powerful and early indicator of infestation. They found that some sheep exhibited deranged fleece as early as 5 weeks after initial infestation with five lice. In the current study, the pattern of change in fleece derangement reflected lice numbers both across and within years and provided further support for fleece derangement as an indicator of infestation. Although it took many weeks for the difference in fleece derangement to become statistically significant between infested and non-infested flocks, this should not be taken as an indication of the time to detect a new infestation. Some sheep in the infested mobs had fleece rub, which is indicative of infestation, much earlier. For example in Y1, the infestor sheep in Group F1, which was initially infested on Day 135, had a wool rub score of 2.0 at the next inspection compared with a mean rub score across groups of 0.09. The sheep with the second highest final louse count in this group had only two lice detected at the penultimate inspection on Day 329, but a density of 3.0 per part at the final inspection 7 weeks later and corresponding wool rub scores of 1.0 at Day 329 (compared with an average of 0.09) and 3.5 at the final inspection (compared with the mean score of 0.3). In practice, a few sheep rubbing could indicate the presence of lice to a grower who could then confirm the presence of lice in the flock by inspecting the suspect animals. The proportion of the flock showing fleece derangement is now used in a module of a web-based decision-support tool for producers (LiceBoss, http://www.wool.com/Grow_LiceBoss.htm, verified 20 June 2011) to estimate the degree of infestation present and to assist the determination of whether or not a long wool treatment is likely to be economically justified (Horton *et al.* 2007).

Effect on production characters

Quantification of the production loss likely to be caused by lice in different situations is crucial for the development of optimal control strategies. The main economic character affected in the present study was clean wool weight. In Y1, the group infested at 4 months cut 0.12 kg per head less than did the non-infested sheep ($P < 0.05$). In both Y2 and Y3, when lice numbers were higher and the sheep infested longer, there was an advantage of 0.22 kg per head in favour of the non-infested sheep. This is our best estimate of the loss that would be expected in a spring-shorn flock that becomes infested soon after shearing in environments similar to that of western Queensland. In Y2, louse numbers in Group S2 reached much higher levels than in any of the other groups (8.5 per part), and in this group, clean fleece weight was reduced by 0.69 kg per head compared with the mean cut in the uninfested groups. This group was infested both from a carry-over infestation and the introduction of a lousy donor sheep. This supports the assertion often made that it is in the second year of an infestation that the main economic loss from lice is experienced and underlines the importance of closely inspecting a flock for lice at shearing before making the decision not to treat.

The other major determinant of wool value is fibre diameter. Although there was a significant difference between the infested and non-infested flocks in fibre diameter in Y2, this result is at variance with findings in other studies (Wilkinson *et al*. 1982; Niven and Pritchard 1985; Cleland *et al*. 1989) and there was no difference in the other years or in the cross-over analysis. In addition, the difference was small (0.6 µm) and there was no apparent effect on fibre diameter in the most heavily infested group (S2) in Y2. The reason for the significant difference in Y2 is uncertain but was more likely to be an experimental artefact than the effects of infestation.

Other production characters affected by lice in the present study were generally similar to those in previous studies (reviewed by James 2008). Greasy fleece weight was heaviest in the non-infested groups in all years except Y2, although the difference was only significant in the cross-over analysis. Yield was lower in the infested groups, although only by 3% in the cross-over analysis, and this contributed to the lower clean fleece weights observed in the infested groups. Lice had no effect on bodyweight gain, which was also the case in all previous studies (Kettle and Lukies 1982; Wilkinson *et al*. 1982; Niven and Pritchard 1985). The significantly shorter fibre length we observed in the infested groups in Y3 could have been the result of rubbing and biting in response to lice. A relatively greater change in staple length from Y2 to Y3 in Group S2, which had higher louse numbers in Y2, also suggests an effect on staple length in heavier infestations. There was no difference in staple strength between infested and non-infested sheep, which is in accord with the results of previous studies (Hansford 1987; Cleland *et al*.1989).

Although classer scores indicated more yellowness in the fleeces from infested sheep, there was no difference in objectively measured clean wool colour, suggesting that it would not have affected the quality of the processed fibre. This apparent conflict is possibly not surprising because there is often a poor relationship between greasy and clean (scoured) wool colour (James *et al*. 1990). Cotting observed in the infested groups may have affected the processing performance of the wool because previous studies have reported more cotting, higher card loss and lower top to noil ratio in wool from infested flocks (Wilkinson *et al*. 1982; Cleland *et al*. 1989). However, the level of infestation was lower in our studies than in those noted above and most of the wool assessed as cotted was Score 2 or medium cott, with only 11% classified as hard cott in Y2 and 14% in Y3.

Because higher proportions of fleeces from infested sheep were classed into lower wool lines, infestation could have affected the price received for the wool at sale. However, because there were only minor effects on measured wool-quality characters, the effect on wool price would have been strongly influenced by the method of sale and the relative importance of subjective and objective assessments in price determination.

Taken overall, it appears that if lice are not present at shearing, even if they subsequently enter the mob, in many instances they will not build to levels where serious economic loss will be experienced before the next shearing. This may be particularly so with spring-shorn flocks running in areas with high solar radiation during summer. These results underline the importance of taking an economic threshold approach to the application of long wool treatments to avoid unnecessary cost and potential undesirable side effects. This can now be done by using the Long wool module available on the LiceBoss decision-support website (http://tools.wool.com/Liceboss/liceboss/LongWoolDss/, verified 20 June 2011).

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