Biology and population dynamics of sheep lice: implications for control

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Summary
Knowledge of the biology of the target pest is essential to the design of efficient control programs. However, information is lacking on many important aspects of the basic biology of sheep lice (Bovicola ovis) despite recommendations of the need for research in this area from past workshops. In this paper we summarise some of the more recent information on transmission and population dynamics of sheep lice and discuss implications for control. We also describe factors which may regulate these processes and highlight some specific areas in which information is required.

Keywords
Phthiraptera, *Bovicola ovis*, transmission, survival, regulation.

Introduction

For most of this century lice have been controlled almost exclusively by chemical methods and regulation. Difficulties associated with chemical use have meant that it is now important to develop alternative or more insecticide efficient methods of control. The key element in planning integrated approaches to pest control is good knowledge of the biology of the target organism. However, relatively little study of the basic biology of sheep lice has been carried out and many of the ‘facts’ on which we base recommendations come from anecdote rather than hard evidence. Even though we have designed programs which incorporate elements such as preventing the introduction of infested sheep, quarantining introduced sheep and monitoring for lice, much of the biology on which to base recommendations on the conduct of these procedures is missing. The first recommendation from the last major workshop on sheep louse control in 1988 (Anon, 1988) was the need for “a research project to examine the basic biology of *Damalinia (Bovicola) ovis*…” Although some gains have been made, this recommendation remains substantially unaddressed. In this paper we summarise some of the more recent work on the biology of lice and highlight some specific areas where information is needed. More comprehensive reviews are given by Arundel and Sutherland (1988) and James (1999a).

Intuitively, sheep lice should be easy to control. Consider the following aspects of their biology:

Obligate parasites with no off host stage: Sheep are not subject to continual challenge from free living stages as with other parasites such as helminths, blowflies and ticks. All stages live on the host and the whole population in a flock or on a property is potentially subject to the effect of control procedures imposed on the sheep.

No other functional hosts to act as reservoirs: Although *B. ovis* have been shown to be able to complete a life cycle on goats (Hallam, 1985), in practical terms goats are unlikely to be important in causing infestations in sheep.

Slow intrinsic rate of increase: Females lay at a maximum rate of about 2 eggs every 3 days and, in laboratory colonies, have mean (maximum) adult lifespans of 49.5 (74) and 27.7 (53) days for males and females respectively (Hopkins and Chamberlain, 1965). This suggests that a female is likely to lay approximately 19 eggs in her lifespan. It should be noted that these figures are derived from laboratory colonies and it is uncertain how well they correspond to the situation on sheep.

Susceptible to regulating influences: A relatively low daily mortality of nymphs and adults is sufficient to prevent population increase (Murray and Gordon, 1969) (see Figure 2).

Long residence time on the host (compared to parasites which only visit intermittently to feed or which complete the on-host stage in a few days): This characteristic may be important with immune based or other similar approaches to control where the aim may be a long term reduction in viability or where the response takes some time to develop.

Narrow environmental tolerances: Lice are very susceptible to environmental influences. Temperatures between 30°C and 40°C are required for female *B. ovis* to lay eggs and for the eggs to complete development (Murray, 1960). All stages of lice are killed when exposed to 48°C for 60 min, 50°C for 30 min. or 55°C for 5 min (Murray 1968) and high solar radiation during summer can cause temperature gradients in the fleece from 70°C at the fleece tip to 45°C near the skin within 5 to 10 minutes of exposure. In addition, Murray (1968) suggests that significant mortalities may also be caused by rapid reversal of temperature gradients in the fleece as sheep walk from shade into sunlight. Eggs fail to hatch at humidities above 90% and if the fleece remains saturated for more than 6 hours many nymphs and adults can drown (Murray 1963).

The assertion that lice should be easy to control may seem puzzling given the apparent difficulty in eradicating lice. However, these difficulties relate more to spatial problems such as ensuring that all infested sheep are treated and all potential lice breeding areas on each treated sheep receives an active concentration of insecticide. In recent years marked advances have been made in improving application methods for chemicals (Lund *et al.*, 1994; Lund *et al.*, 1997). However, in most instances control still relies on completely covering every sheep in a flock or on a property with insecticide. As market forces tighten restrictions on chemical use, a better knowledge of louse biology will be required to develop strategic approaches to chemical use and alternative methods of control.

Transmission of lice

A key element of any louse control program is the prevention of new infestations. This is particularly important on properties where managers are changing from routine annual treatment and sheep will not benefit from the residual period of protection provided by post shearing applications. In addition, an infestation soon after a woolgrower has decided to change to a treatment on detection regime often leads to loss in confidence in this approach and a return to annual treatments.

By far the most important source of infestation will be contact with other infested sheep, specifically strays and purchased or agisted sheep. However, sheep owners often ask about the possibility of sheep becoming infested from sources such as contaminated handling facilities, wool on fences, or the clothing of shearers and sheep handlers. To answer these questions we conducted a series of experiments to assess the possibility of infestations from these sources.

Survival of lice away from sheep

Obviously a critical factor in the likelihood of infestations beginning from non-sheep sources is the period for which lice can live away from sheep. Although the standard statement is that lice will not survive for more than 4-5 days after removal from sheep, it now seems that the potential period of survival is much longer than this.

Laboratory studies were conducted to investigate the relative periods of survival of the different life stage of *B. ovis* and the effects of temperature and the presence of wool on survival period. Large nymphs survived significantly longer than both small nymphs and adults and both age groups of nymphs survived longer than adults. This pattern was consistent across all temperatures. In a comparison of survival at 4°C, 20°C, 25°C and 36.5°C lice consistently lived longest at 25°C and lice lived significantly longer at both 20°C and 36.5°C than at 4°C. The survival periods measured at 25°C are shown in Table 1. Complete results are presented by Crawford *et al.* (2001).

The lice in the first study (Table 1) were provided with approximately 12 fibres of raw wool as a substrate. In a subsequent experiment, lice in vials were given 0.07g of either raw or scoured wool. Lice lived significantly longer on the unscoured wool and it was in this experiment that the maximum periods of survival for the study were observed. One nymph collected from a sheep survived for 29 days and one female adult from a laboratory colony survived for 28 days.

Table 1. Survival of small and large nymphs and adult B. ovis at 25°C

	LT50* (days)	95% fiducial limits	LT90 (days)	95% fiducial limits	Days to 100% dead
Small nymphs	6.6[c]	6.0 – 7.3	15.9[c]	14.2 – 18.5	19
Large nymphs	8.8[b]	6.3 – 11.8	24.1[b]	16.5 – 59.2	20
Adults	5.9[b]	4.1 – 7.7	11.7[a]	8.9 – 22.1	15

To examine survival under conditions more likely to be encountered in practice, lice were placed in tubes with approximately 12 fibres of unscoured wool in the catching pens of shearing sheds at Turretfield Research Centre (September and October) and Urrbrae Agricultural High School (April and May). Temperatures varied between 2.2°C and 31.2°C in the Turretfield study and 7°C and 26°C in the Urrbrae study. The results are shown in Table 2. Even though temperatures were less than optimum, lice survived for up to two weeks in most instances.

For the lice to constitute a threat for infestation they must still be viable and able to develop to adults in the case of nymphs and produce fertile eggs in the case of adults. Nymphs and adults were held away from sheep at 20°C and 25°C until 80% of them died. Those still alive were then provided with sheep skin scrapings and monitored to see it they would survive and breed. In nearly all cases nymphs developed to adults and adult females produced viable eggs.

Table 2. Survival of lice in shearing sheds at Urrbrae Agricultural High School and Turretfield Research Centre.

	Shearing Shed	LT50 (days)	95% fiducial limits	LT90 (days)	95% fiducial limits	Days to 100% dead
Females	UAH*	3.0[a†]	2.3 – 3.8	6.9[abcde]	5.4 – 10.5	9
	TRC	5.2[b]	4.9 – 5.5	8.6[abc]	8.1 – 9.2	14
Males	UAH	3.3[ac]	2.6 – 4.0	5.8[ab]	4.8 – 9.0	7
	TRC	4.9[b]	4.7 – 5.1	7.3[abd]	6.9 – 7.8	12
Nymphs	UAH	4.2[c]	3.8 – 4.5	8.7[abc]	8.0 – 9.6	14
	TRC	6.3[d]	5.9 – 6.6	10.9[ae]	10.3 – 11.8	16

* UAH = Urrbrae Agricultural High School; TRC = Turretfield Research Centre

† Means from 3 replicates. LT50 and LT90 values followed by different letter superscripts are significantly different (from Crawford *et al.* 2001).

Transmission from other sources

Wool on fences: Three studies were conducted to assess the possibility of sheep becoming infested from wool rubbed onto fences by lousy sheep. Lice were seeded into wool staples, the staples then attached to a fence and the number of lice in each staple monitored. Most lice dropped out of the wool within 1 hour. Only 2 of a total of 225 lice were still present in the wool on the fence after 24 hours, suggesting that transmission of lice to sheep from wool on fences is unlikely.

Transmission on the clothing of sheep handlers: Footwear is seldom washed and seemed the most likely article of clothing on which lice may be transmitted. A number of trials were conducted in which sheep known to be lousy were held in a shearing position by a shearer wearing moccasins for 3½ minutes, the approximate time it takes to shear a sheep. The moccasins were then closely examined and the number of lice counted. Up to 124 lice per moccasin were found, demonstrating that lice can readily transfer during this time. Lice survived on these moccasins for up to 10 days. Microwaving moccasins for 5 minutes or leaving them in a freezer overnight reliably killed all lice.

This work has been interpreted in some areas as ‘shearers are spreading lice’. If louse infestations are below clinical levels, the likelihood of transfer of lice by this means is low. However, if shearers or other people contacting sheep are aware of lice on a property, precautions should be taken to prevent the spread of lice to louse free flocks on clothing or footwear.

Transmission on other insects: Many mallophagan species have been found to exhibit phoretic behaviour (Keirans, 1975). In these cases the smaller biting lice attach by their mandibles to the legs or bristles of larger flies. Most previous studies have focussed on lice inhabiting avian hosts, but Bay (1977) reported a case of phoresy of *Bovicola bovis* (L.), the cattle biting louse, on the buffalo fly (*Haematobia irritans*). A preliminary study was conducted with sheep blowflies (*Lucilia cuprina*) using 5 mm diameter plastic vials connected by a 45 cm long, 2 cm diameter plastic tube (Crawford, 1999). Approximately 300 lice of mixed sex and stage were placed into one of the two vials with *L. cuprina* adults. Numbers of flies ranged between 10 and 18 in the different trials. In five runs with this apparatus, 2,2,1,0 and 5 lice transferred. *L. cuprina* constantly groomed themselves and in most instances rapidly removed lice which attached to their legs. The low numbers of lice which transferred despite the high level of contact between the flies and lice suggest that this is not likely to be a major form of transmission. However the results demonstrate that phoretic transfer is possible and should not be completely discounted as a means of spread.

Population dynamics

The rate of build up of lice in a mob and knowledge of the factors which affect this is critical for the following reasons:

(a) Assessment of the likelihood of lice building to numbers where economic losses are experienced before the next shearing and to determine if a midseason treatment is justified

(b) Determination of the time for which sheep need to be quarantined for a reasonable degree of certainty that they are not infested. Critical to this is knowledge of the level of infestation at which fleece derangement becomes apparent and at which lice are likely to be detected. (Studies are currently in progress to assess the time from initial infestation until sheep start to exhibit signs of lice and how this varies between sheep)

(c) The potential utilisation of natural regulatory influences as part of integrated control programs. This may be for the strategic use of chemical applications or for the combination of a range of regulatory factors to prevent population build up.

Build up of an infestation in sheep is the combination of spread amongst sheep and increase in louse numbers on individual sheep. Most infestations begin from one or a few sheep in the mob and then spread to the rest of the flock. Although Cleland *et al.* (1989), Elliott *et al.* (1986) and Wilkinson *et al.* (1982) have investigated the spread of lice in flocks, with the exception of the excellent work of M.D. Murray during the 1960's there has been little investigation of factors that influence sheep lice dynamics.

How many lice does a sheep have?

For population modelling and determination of the relationship between louse numbers and time until detection it is important to be able to relate the number of lice counted per part to the absolute lice numbers on sheep. James and Moon (1999) assessed this relationship in two ways. Four sheep were weighed, killed, skinned and the skins marked into regions including the head, neck, back, foreleg, sides, hindleg, lowleg, and belly. The area of skin in each region was measured and relative densities of lice in each region estimated from louse counts on live sheep. The total number of lice in each region was then estimated by assuming that each 10 cm part exposed 3 cm surface area, calculating the number of 3cm ^{2} units in each region and multiplying by the relative density for that region.

Secondly, areas of 10 cm x12 cm were marked at nine body sites on each of three infested sheep. Five 10 cm fleece partings were made across each area and the number of lice counted. The wool was then clipped from each area with fine animal clippers and the number of lice remaining on the skin recorded. Lice were extracted from the wool samples in Berlese funnels with 100W bulbs for 4 hours and then the sample dissolved in boiling sodium hydroxide and examined for the exoskeletons of any remaining lice. Linear regression models were fitted with x as mean number of lice per 10cm wool part and y as either lice alive (counted on skin + Berlese extraction) or total lice (lice alive+NaOH extraction) per 100cm^2 area. The total number of lice calculated by the two methods for a small sheep (estimated wool bearing area of 1m^2) and large sheep (estimated wool bearing area of 1.5m^2) are shown in Table 1.

Table 3. Estimates of the numbers of lice on small and large sheep with louse densities of 1 and 10 lice per part.

	Small sheep ($1.0\ m^2$)		Large sheep ($1.5\ m^2$)	
	Mean lice per part on the sides			
	1	10	1	10
Estimated geometrically	1,868	18,653	2,798	27,979
Estimated from regression	2,015	20,141	3,021	30,208

(Adapted from James and Moon, 1999)

Spatial distribution of lice

One of the areas of biology specified in the recommendations from the 1988 lice control workshop was the temporal and spatial distribution of lice in treated and untreated sheep at various times in relation to shearing and treatment. James and Moon (1999) counted lice at 69 body sites at approximately monthly intervals and describe the louse densities in different body regions and how these changed through the season. Highest densities of lice were found along the sides at most times of the year, suggesting that this is where inspections should be concentrated when trying to detect lice. Significant numbers of lice were found on the head and in the wool on the sides of the face, particularly when the wool was longer, underlining the importance of ensuring that active levels of insecticide are delivered to these areas when treating for lice. Shearing markedly reduced the overall density of lice but also changed the distribution of lice with a greater proportion of lice lower on the body, particularly on the neck, lower flanks and legs. Densities increased on the neck after shearing in both years suggesting that lice actively migrated into this region on shorn sheep.

Kettle *et al.* (1983) and Johnson *et al.* (1995) showed that deltamethrin from backline formulations reached more distant sites in concentrations that were lower than close to the point of application, but neither study investigated concentrations on the ventral side of the neck, belly or legs. Concentrations of insecticide applied by sheep showers are also lower on the lower body regions and under the neck (Kirkwood *et al.*, 1978). Movement of lice into these regions after shearing may help to explain the treatment failures often experienced. In addition, Johnson *et al.* (1995) noted that maximum concentrations of deltamethrin from backline treatment were not achieved at sites on the lower flanks for 4 to 11 days. Migration of lice to areas of low chemical concentration, perhaps further stimulated by an advancing front of irritant chemical in the case of synthetic pyrethroids, would be a powerful mechanism of selecting for resistance.

Improving the delivery of insecticides to the lower parts of the sheep's body would increase the chance of eradicating lice when sheep are treated after shearing and should reduce selection pressure for further resistance.

Spread of lice amongst sheep

Three studies have been conducted in which the rate of spread from one or two initially infested sheep can be compared. Elliott *et al.* (1986) paddocked one sheep infested with 4,000 lice (ca. 1-2 lice per part) with 19 clean sheep carrying nine months growth of wool. Three months later, 35% of these sheep were infested. Cleland *et al.* (1989) paddocked two moderately infested sheep with 50 clean wethers with 9 months wool and at 17 weeks, 26% were detected with lice. James *et al*. (2001) paddocked one moderately infested sheep with 32 ewes with 10 weeks wool and 15 weeks later, 53% were infested. It should be noted however that this is the cumulative percent infested. Lice were actually detected on 41% of sheep at this inspection. Elliott (1988) cites one instance in which a heavily infested sheep was paddocked with 80 clean sheep and 65% were infested within a month and all were infested after 5 months. These studies indicate that the rate of spread can be highly variable.

In the study of Cleland *et al.* (1989) the sheep were shorn at 20 weeks and by the next shearing 12 months later all sheep were infested, 48% with a heavy infestation and 52% with a medium infestation. The sheep were shorn at 3 months in the study of Elliott *et al.* (1986) and at the next shearing 12 months later, 35% of sheep had a heavy infestation and the rest had light or medium infestations. In the study of James *et al*. (2001) the infestation was allowed to develop from introduction of the lousy sheep until shearing of the ewes at 51 weeks. At this time all sheep had lice, 19% with a light infestation, 65% with a medium infestation and 16% with a heavy infestation. Thus if a mob is infested at shearing, but the infestation is not detected and the sheep remain untreated, it can be expected that in the absence of a midseason treatment significant wool losses will be experienced by the next shearing.

As the number of growers using routine annual treatments decreases it might be expected that the incidence of midseason infestations will increase. Thus the concept of action thresholds often used in pest management will become more important and decisions will need to be made on whether or not it is economically beneficial to treat sheep in long wool or better to leave them until the next shearing when eradication can be achieved. Models for louse build up similar to that used by James *et al.* (2001) but developed for different situations and linked to production data, are needed.

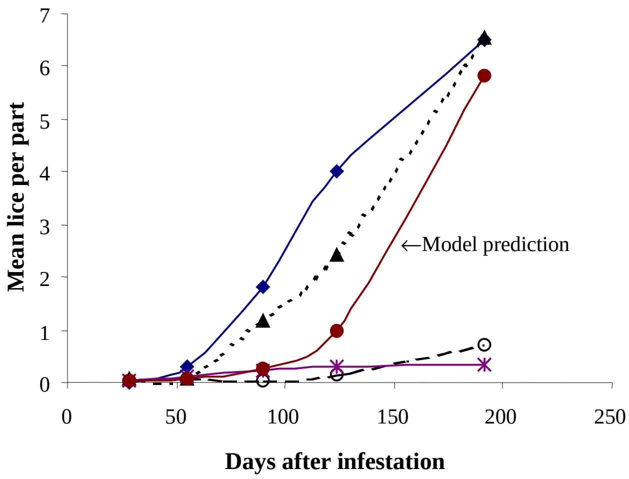

Figure 1. Build up in louse numbers on four sheep following infestation with equal numbers of lice and as predicted by a population model

Build up on individual sheep

The second component of louse population build up in a mob of sheep is increase on individual sheep. For most of the year lice live in a very favourable environment. They are well insulated from environmental conditions and host grooming by the thick layer of wool carried by most sheep and they are kept at a steady warm temperature by the sheep's body heat. The major disruption to this is from shearing. However, there are large differences in the rate at which lice build up on different sheep, even after a standard infestation. Figure 1 shows build up of lice on 4 Merino sheep following infestation of all animals in a mob of 42 ewes with 20 female, 10 male and 5 nymphal lice on two occasions a month apart. Sheep numbers 17 and 44 had the highest rated of build up and sheep 69 and 170 the lowest. These differences have significant implications for control procedures and the biological mechanisms which underlie them require clarification.

Also shown in Figure 1 is the rate of build up as predicted by a population model assuming an egg laying rate of 0.67 eggs per day, egg fertility of 70%, daily nymph survival of 99%, daily survival of adults and preovipositional adults of 100% and assuming that mature female lice live for 30 days. These estimates are derived from Scott (1952), Murray (1960) and Hopkins and Chamberlain (1974). The rate predicted by the model closely approximates the rate on the two sheep with the greatest rates of increase in Figure 1, which is what would have been expected given that we did not impose any regulating factors other than density dependence in the model. The results of Wilkinson *et al.* (1982) show that lice can build from an initial infestation of 10 lice to light infestation (1 louse per 10 cm wool part) in 6 months. Our model predicted that it would take 170 days for the population to increase from 10 lice to 2,500 lice, which approximates the number of lice on an average size sheep with an infestation of 1 louse per part.

The other point to note is that, as mentioned earlier, *B.ovis* appears to be very sensitive to regulating influences. Figure 2 shows the implications of imposing a daily mortality of 5.5% on nymphs and adults following the initial infestation of a sheep with 20 female, 10 male and 5 nymphs. This suggests that the population is precariously balanced and that identification and manipulation of regulating factors could play an important part in an integrated control program.

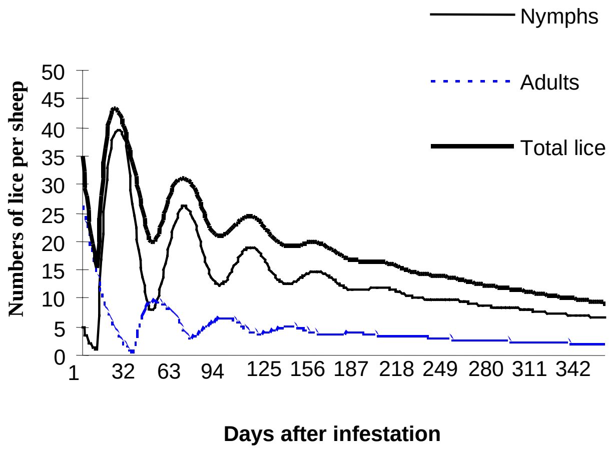

Figure 2. Model-predicted effect on louse numbers of a daily mortality of 5.5% in nymphs and adults after initial infestation with 35 lice.

Regulating influences and their potential for use in control

Integrated programs aim to utilise a range of control approaches in a way which makes most use of natural regulating influences, or at least does not disrupt them. As discussed elsewhere in these proceedings (Karlsson *et al.*), IPM programs may utilise physical, cultural, biological and genetic (host resistance and genetic manipulation of pest populations), as well as chemical means. However, there has been little research to investigate the use of these approaches for controlling lice.

Physical and cultural mechanisms: Shearing is a powerful regulating influence and can remove up to 66% of the population (Heath *et al.* 1995). It also exposes the remaining lice to environmental influences and many more die subsequently. It is likely that time of shearing influences the amount of post shearing mortality of lice, although there appear to have been no studies of this. The likelihood of eradicating lice with post shearing treatments may be greater at some times of the year.

Saturation of the fleece kills a large proportion of lice. Murray (1963) observed reductions in louse numbers in excess of 90% on some sheep following a thunderstorm. Heath *et al.* (1995) reduced louse numbers in Romney sheep with 30 mm wool by up to 35% by jetting with water. Shearing and dipping with water reduced louse burdens by up to 89%. The addition of detergent to the water gave no significant improvement over water alone when either jetting or dipping. In a South Australian study, jetting long wool Merinos with water and with a commercial insecticidal soap solution (Natrasoap®), gave reductions in louse numbers of 33% and 67% respectively (Richards and James, unpublished).

As lice spread by sheep-to-sheep contact, management practices which increase contact between sheep, particularly where sheep are penned together for extended periods of time, are likely to increase the rate of build up in louse infestations. Where an infestation is found and no treatment can be implemented before the next shearing, reducing the frequency of these procedures will slow population build up and reduce the potential for wool losses. Minimising the frequency of yarding sheep may also add to the effect of long wool treatments when there is a possibility of resurgence in the louse population before the next shearing.

The action of magnesium fluorosilicate approved for use in some organic systems is apparently largely physical. However, commercial products generally include rotenone which contributes to the insecticidal effect. In addition microwaving and freezing have been shown to be lethal to sheep lice and can be used to disinfect clothing or footwear (Crawford *et al.*, 2001).

Biological agents: There has been little investigation of the possibility of biological control of lice. Few pathogens or parasites of either mallophagan or anopluran lice are reported (Ward, 1977) and personal observation suggests little evidence of epizootics in sheep louse populations. The only significant investigation of a biocontrol agent for lice is the potential use of *Bacillus thuringiensis* (B.t.) (Gingrich *et al.,* 1974; Pinnock, 1994; Hill and Pinnock, 1998). One note of particular interest here is that B.t was found to be most effective against strains of lice which were resistant to synthetic pyrethroids (Drummond *et al.* 1995). Preliminary studies have shown that the fungus *Metarrhizium anisoplae* will infect sheep lice (Leemon, *pers. comm*.) and the fungus *Trenomyces histophtorus* has been shown to infect other species of mallophagan lice (Meola and Devaney, 1976). In addition, the entomopathogenic nematode *Steinernema carpocapsae* will invade and kill lice under suitable conditions (James and Bartholomaeus, unpublished). Inundative biocontrol of lice would seem to be a possibility and warrants further investigation.

Host resistance: There is substantial and significant variation in susceptibility to lice amongst sheep, both between and within breeds. Some (non-merino) sheep appear to be able to resist infestation (James *et al.*, 1998a). Degree of susceptibility also appears to be affected by nutrition and disease with sheep in poor condition more likely to develop heavy infestations of lice. In addition, despite their superficial habit, lice stimulate an immune response and there is some evidence that this may play a part in regulating louse populations (James *et al.*, 1998b; James, 1999b). The possibility of increasing resistance to lice by breeding, vaccination or nutritional supplementation should be investigated.

Conclusion

There is a paucity of information on the basic biology of sheep lice and there has been very little research into non-chemical methods of control. Lice are obligate parasites, with all stages spent on the sheep, and no other functional hosts. From our knowledge to date they are very susceptible to regulating influences. It seems that research into the biology of lice with an aim to developing more insecticide efficient approaches or new methods of control would have a high probability of success.

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