

# Distribution and ecology of the lucerne flea, *Sminthurus viridis* (L.) (Collembola: Sminthuridae), in irrigated lucerne in the Hunter dairying region of New South Wales

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## Abstract

The lucerne flea, *Sminthurus viridis* (L.), is shown to be a pest of irrigated lucerne in the summer-rainfall, temperate-type climate of the Hunter region in New South Wales, an area previously considered unsuitable for its establishment. Main activity occurred at average temperatures  $\leq 13\text{--}15^\circ\text{C}$ , resulting in five generations per season. Establishment and activity were closely related to irrigation. Eggs hatched throughout summer but populations failed to develop. It was unclear if diapausing eggs, the progressive hatching of non-diapausing aestivating eggs or both helped the species survive to form viable populations in winter. Early activity was detected from catches of very small nymphs ( $< 0.3 \pm 0.14$  mm) in pitfall traps, which preceded lucerne flea presence as small nymphs ( $< 0.82 \pm 0.15$  mm) on plants by approximately 2 weeks following irrigations or major rainfall. Predators and grazing by dairy cattle had no effect on lucerne flea numbers. Significant relationships were established between the lucerne flea and several plant growth and damage factors.

**Key words** biology, establishment, pest–plant relationships., temperate-type climate.

## INTRODUCTION

The lucerne flea, *Sminthurus viridis* (L.), is an important pest of pastures in the essentially Mediterranean-type climates of southern Australia. Based on laboratory data, it has been proposed that other areas, including the temperate central-eastern coast of New South Wales (NSW) are favourable for establishment (Maclagan 1932). However, Wallace and Mahon (1971) deemed that incursions into coastal NSW were likely to be temporary, based on the absence of critical temperature, moisture and host plant conditions that allow the species to survive summer through diapause in aestivating eggs (Davidson 1934; Wallace 1968). Wallace and Mahon (1971) regarded that northerly and easterly spread in NSW would be approximately limited to the 250- and 225-mm isohyets, respectively.

Temperature and moisture also influence development and numbers of lucerne flea when the species is active locally between autumn and spring. Temperatures between 11 and 15°C are regarded as optimal (Davidson 1934), while those higher than 25°C are inhibitory (Wallace 1967). Relatively high moisture levels are necessary, although drowning or reduced oviposition in saturated soils may occur (Johnston 1960). Adequate moisture is commonly maintained across southern Australia by winter rainfall patterns and the dry summers promote the production and survival of aestivating eggs. However, Wallace and Mahon (1971) suggested that irrigation could compensate for deficiencies in rainfall in winter and help provide isolated patches at other locations that would otherwise be unsuitable for establishment. Survival, numbers

and local distributions in new areas would then be dependent on soil type, the composition and density of plants in pastures, and density-induced mortality in the lucerne flea populations (Wallace 1957, 1967).

The lucerne flea has already spread beyond the limits predicted for NSW. Presence and damage to lucerne crops has been common in irrigated areas along river flats on the western and northern tablelands and slopes (Bishop *et al.* 1991). Originally found only in a few areas and on a few farms east of the Great Dividing Range (Wallace & Mahon 1971; Bishop 1991), the lucerne flea now appears to be of increasing importance in pastures of the Hunter dairying region, most of which is coastal (Launders *et al.* 1997). This supposedly unsuitable area is reliant on pure and mixed stands of irrigated lucerne for milk production. The aims of the present study were to investigate the distribution of the lucerne flea in irrigated lucerne in the Hunter region and describe aspects of its ecology that may be relevant to ecologically based control strategies. The present paper considers distribution and ecology, while control is addressed in Bishop *et al.* (2001).

## MATERIALS AND METHODS

### Lucerne flea survey

A survey of the distribution of the lucerne flea was carried out from 25 randomly selected farms in the Hunter dairying region. These farms represented nine zones in the Hunter Valley (20 farms), Dubbo (two farms) and Tamworth (three farms) areas. Samples were taken from old ( $> 2$ -year-old) and new ( $< 2$ -year-old) pure lucerne stands at each farm in

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March/April (autumn) and July/August (winter) 1997. Vacuum samples (Holtkamp & Thompson 1985) were taken from three randomly selected 1.0-m<sup>2</sup> sites in each lucerne stand. Collections were placed separately in plastic bags and returned to the laboratory, where the lucerne fleas were killed with ethyl acetate and separated from plant material by sieving and from other insects by counting under a binocular microscope.

A generalised linear mixed model (Schall 1991) with log-link function and gamma-error distribution was fitted to the data. The model fitted was:

$$\log_e(\text{count}) = \text{zone} + \text{age} + \text{season} + \text{zone.age} + \text{zone.season} \\ + \text{age.season} + \text{zone.age.season} + \textit{farm} + \textit{site.farm.rep},$$

where the italicised terms were included in the model as random effects. Predicted means were separated by using the least significant difference procedure.

### Lucerne flea ecology

Studies were carried out on irrigated lucerne (cv. Aurora) near Singleton (32°36'S, 151°13'E) in the Hunter Valley from 1997 to 1999. In the first study, data were taken from unsprayed plots (12 m by 12 m) arranged in Latin squares with three insecticide treatment strategies, which used chlorpyrifos sprayed at different times, each replicated six times. Sites were changed each year because of alterations to cropping and differential damage to the plots in each season. Blocks were rearranged at each change of site. A vacuum sample was taken from two 0.25-m<sup>2</sup> quadrats per plot each week in the 1997 season, every second week in the 1998 season and approximately monthly (within 2 weeks of irrigation) during summer 1997–1998. Counts were expressed as numbers per 1.0 m<sup>2</sup>. A single pitfall trap (1-L plastic jars with 8-cm diameter openings) was placed in each unsprayed plot in the 1997 season. These traps were charged with 100 mL 4% formaldehyde, covered to prevent rainfall and debris from entering and catches were collected weekly. Insects were removed from debris and plant material in each vacuum and pitfall trap sample by sieving and were then identified and counted under a binocular microscope. Numbers of lucerne flea, aphids [bluegreen aphid *Acyrtosiphon kondoi* Shinji, cowpea aphid *Aphis craccivora* Koch, pea aphid *Acyrtosiphon pisum* (Harris) and spotted alfalfa aphid *Therioaphis trifolii* Monell f. *maculata*], spiders (all species combined) and two species of potentially predatory mites (*Bdellodes affinis* Atyeo and *Micromaris* sp.; Bishop et al. 1998) were recorded. Numbers of lucerne fleas were initially divided into the following size categories (stages) in lieu of a more accurate means of separating instars: small nymphs (< 0.82 ± 0.15 mm); medium-sized nymphs (0.82 ± 0.15–1.94 ± 0.13 mm); large nymphs (> 1.94 ± 0.13 mm); and adults. A fifth stage (very small nymphs, < 0.3 ± 0.14 mm) was found in pitfall traps and was rarely evident on plants.

The data were used to graphically compare changes in numbers and stages (expressed as proportions of the total

lucerne flea count) of the lucerne flea in relation to average weekly temperatures, total weekly rainfall (recorded by NSW Agriculture at Singleton) and normal farm management. They were also used to compare lucerne flea counts and the composition of stages (proportions) recorded by the two sampling methods in 1997; analysis of variance was applied to the logit-transformed proportion data at the start of the 1997 season only. No differences were observed thereafter. Correlation analysis was used to compare trends in numbers and stages sampled by both methods over the 1997 season. Correlation analysis was also used to describe the relationship between irrigation/rainfall and hatchings (taken as the peaks in numbers of all nymphs < 0.82 ± 0.15 mm) using the vacuum and pitfall sampling methods. Student's *t*-test was used to compare the times from irrigation/rainfall to the detection of peak numbers of very small nymphs in pitfall traps and small nymphs in vacuum samples. The third use we put the data to was to relate changes in numbers of the predatory mites and the spider complex to numbers of lucerne flea and aphids; correlation coefficients were calculated to describe relationships between lucerne flea, predatory mite, aphid and spider populations. Significance was taken at *P* < 0.05 in all analyses.

The effects of lucerne flea on plants were considered at the second and third harvests of the 1997 season. Different population densities (expressed as cumulative weekly counts in each harvest cycle) and damage levels were obtained from the unsprayed and insecticide treated plots. Stem length, leaf number, percentage of the total number of leaves damaged and percentage of damage (i.e. reduction in total leaf area) in the top, middle and lower thirds of stems were recorded from 20 stems randomly selected in each of the 24 plots. The data were graphed, examined visually and the relationships between insect counts and each of the plant variables tested using linear and bent-stick (Lerman 1980) regression analyses.

In the second study, the time at which the lucerne fleas started to increase in number and produce new populations in late summer or early autumn was considered at Mount Thorley, Scott's Flat and Whittingham, which are geographically separated but all located in the Singleton Shire. Each site had a known history of lucerne flea infestation. Mount Thorley and Scott's Flat had stands of pure lucerne. The lucerne flea population at the Scott's Flat site had just become a problem and was sprayed for the first time in 1998. Lucerne was sparse in a predominantly ryegrass pasture at Whittingham as no new lucerne plantings had occurred on the property for several years because of uncontrollable problems with lucerne flea. Sampling commenced in the first week in March 1999 and was continued for varying periods. Single fields were sampled at weekly intervals initially and then every second week after development was confirmed and until sampling was terminated. Five samples of two 0.25-m<sup>2</sup> quadrats were taken at each location with the vacuum sampler with counts expressed as numbers per 0.5 m<sup>2</sup>. Insects were bagged, killed, sorted, identified and counted as before.

## RESULTS

### Lucerne flea survey

Lucerne fleas were present on 24 of the 25 farms surveyed. Significantly higher numbers were recorded in the Tamworth area, during winter and in the paddocks with older lucerne (Table 1).

### Lucerne flea ecology

Total numbers of lucerne flea over the winter period and monthly counts over summer relative to average weekly temperature and total weekly rainfall from April 1997 to October 1998 are given in Fig. 1a. Farm management is given for the autumn–spring periods only. Lucerne flea was reproductively active for approximately 7 months and abundant when average weekly temperatures were at or below 13–15°C. Activity in July/August 1998 was curtailed during a period of major rainfall resulting in minor flooding in the trial area. Major damage corresponded with peaks in numbers and was recorded on two occasions in each year. All harvesting was by grazing with dairy cattle and this had no obvious effect on lucerne flea numbers. Low numbers were recorded consistently throughout the summer period.

Stages are given as percentages of each size category relative to the total population on each sampling date (Fig. 1b). Five distinct generations were observed in each year, including the minor peaks during initial activity in early autumn when activity was not visually obvious and final activity in spring. Those individuals hatching in summer never developed beyond small nymphs. The 1998 population started to develop in late February when average temperatures were approximately 25°C, rainfall was negligible and the lucerne had to be irrigated. Continuity of sampling was disrupted by the need to change sites (the first field was sod-sown with ryegrass), although population development in 1998 appeared to be consistent at each site (Fig. 1a).

Counts from pitfall traps were much lower than from vacuum samples, but differences were not analysed as there was no realistic basis for comparison. However, data taken

by the two trapping methods reflected non-significantly different trends in the distribution of numbers and stages overall. The only difference was when proportions of all nymphs  $< 0.82 \pm 0.15$  mm from pitfall-traps (81.8%) were significantly greater than the proportions of similarly sized nymphs obtained from vacuum-sampled plants (12.1%) at the start of sampling in 1997. Proportions thereafter and of all other stages were similar in all subsequent generations. Possible differences were observed throughout between the occurrences of peaks in very small nymphs (pitfall traps) and small nymphs (vacuum samples). These peaks indicated hatchings and were each highly correlated with times of irrigation or major rainfall over the two seasons ( $r$ -values:  $> 0.99$ ,  $P < 0.05$ ). However, a comparison of the times (weeks) between irrigation/rainfall and these peaks indicated that those from pitfall traps (0.4 weeks) were significantly earlier than those from vacuum samples (2.14 weeks).

The numbers of the potential predators *B. affinis*, *Micro-maris* sp. and the spider complex were also apparently unaffected by the grazing of the lucerne. Numbers of spiders were correlated with lucerne flea numbers in 1997 ( $r = 0.55$ ,  $P < 0.05$ ), but not in 1998. No relationships were established between the mite species and the lucerne flea. Mite numbers were related to aphid populations or species within the aphid complex in both seasons ( $r$ -values were between 0.42 and 0.60,  $P < 0.05$ ).

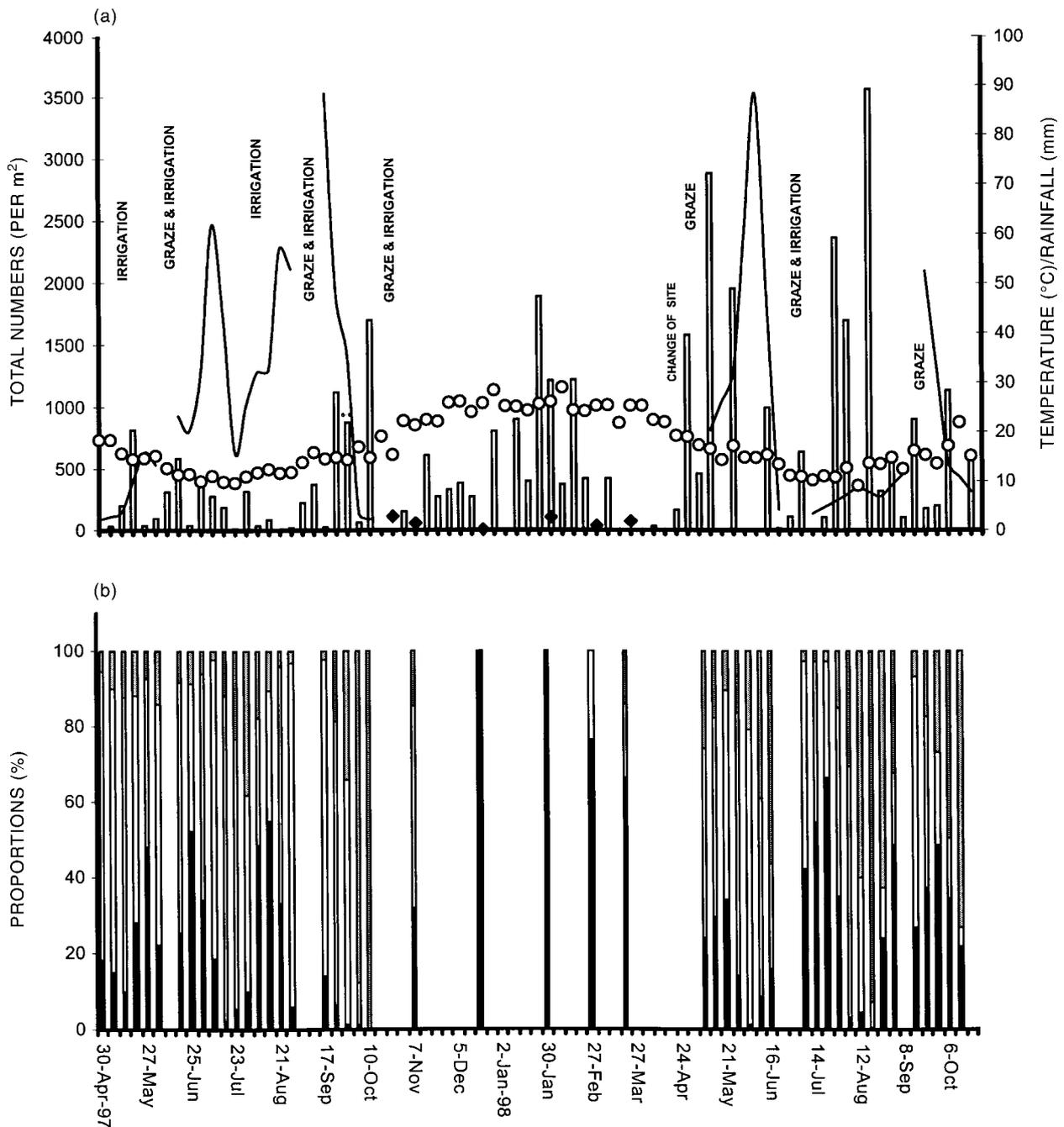
Numbers of lucerne flea were related to most of the plant factors and damage estimates measured in the second and third growth cycles in 1997 (Table 2). Only leaf number was unaffected, although direct damage was mainly to the leaves. Explained variances from the analyses of damage were improved by the change from linear to the bent-stick analysis.

Patterns of activity differed greatly at each of the three sites sampled in 1999 (Fig. 2). Small nymphs were present from the start of sampling at Scott's Flat (Fig. 2a), but failed to establish a viable population until just before activity ceased in October. Similar activity by small nymphs was evident at Mount Thorley in early autumn (Fig. 2b) and a new population was established by early May when average temperatures were approximately 15°C. Although numbers

**Table 1** Predicted mean numbers of lucerne flea per m<sup>2</sup> in the Hunter dairying region of New South Wales derived from surveys of lucerne of different ages at different locations and at different times

Site	Predicted mean number	Age of lucerne		Season	
		Old	New	Autumn	Winter
Denman East	2.5 <sup>b</sup>	1.4	4.0	0.4	8.1
Denman West	7.4 <sup>b</sup>	40.8	0.7	4.1	12.8
Jerry's Plains	4.9 <sup>b</sup>	8.7	2.6	3.8	6.3
Singleton	7.2 <sup>b</sup>	21.1	2.0	6.3	8.1
Singleton East	9.2 <sup>b</sup>	30.9	2.3	8.7	9.8
Muswellbrook	7.3 <sup>b</sup>	12.7	4.0	4.7	10.9
Scone	10.1 <sup>b</sup>	17.0	5.9	3.7	25.5
Dubbo	6.5 <sup>b</sup>	28.7	0.9	4.8	8.7
Tamworth	57.7 <sup>a</sup>	65.2	51.0	13.1	243.5
Overall predicted means		18.1 <sup>a</sup>	3.6 <sup>b</sup>	4.6 <sup>b</sup>	15.0 <sup>a</sup>

Predicted and overall predicted means with different letters are significantly different ( $P < 0.05$ ).



**Fig. 1.** Distributions of (a) total lucerne flea numbers and (b) stages of individuals in the population in relation to average weekly temperatures, total weekly rainfall and farm management at sites near Singleton in 1997–1998. (a) (○), Average weekly temperatures; (□), total weekly rainfall; (◆), monthly lucerne flea count during summer; (—), total numbers of lucerne flea during winter; (b) (▨), adults; (□), medium and large nymphs; (■), small nymphs; irrigation, overhead spray irrigation; graze, harvest by grazing dairy cattle; change of site, relocation of sampling area.

were apparently low at Mount Thorley, the sampling area was part of a larger stand in which lucerne flea damage to one side of the field resulted in the farmer spraying the entire stand twice. Lucerne flea was already reproductively active and in large numbers at the Whittingham site (Fig. 2c) when sampling commenced and average temperatures were between 20 and 30°C. Sampling at Whittingham was terminated in April, that is, the lucerne flea remained active

throughout the season but was ignored by the farmer despite some lucerne flea damage to the ryegrass.

## DISCUSSION

There is a good understanding of the ecological and behavioural constraints on the lucerne flea in the Mediterranean-type

**Table 2** Relationships by two methods of analysis between lucerne flea numbers and lucerne plant factors, estimates of damage and yield at harvest during two growth cycles near Singleton in 1997

Plant factor	Percentage variance accounted for by regression			
	Lucerne growth cycle 2		Lucerne growth cycle 3	
	Linear	Bent-stick	Linear	Bent-stick
Stem length	17.3*	24.9*		
Leaf number	0	11.0		
Percentage of leaves with damage	37.5*	83.6*		
Percentage of damage (top third)	20.0*	50.8*	67.6*	86.5*
Percentage of damage (mid third)	29.4*	63.3*	74.5*	89.9*
Percentage of damage (lowest third)	27.0*	49.5*	77.6*	91.5*
Yield (g 0.5 m <sup>-2</sup> )	26.1*	34.8*		

\*Significant at  $P < 0.05$ .

climates of southern Australia (Davidson 1934; Wallace 1957, 1967, 1968; Wallace & Mahon 1971). Early attempts were made to use these data to predict limits to the species' spread to other areas, but these could not be validated because the lucerne flea was confined within the proposed limits when the predictions were made. We give evidence that now contradicts the proposed limits of spread.

The distribution of the lucerne flea has not been limited to the 225- and 250-mm isohyets in NSW. Establishment beyond these proposed limits has apparently been influenced by irrigation, with most activity on the tablelands and slopes confined to irrigated river flats. Incursions have occurred into the Hunter Valley and these have not been temporary. Establishment in the temperate, summer-rainfall areas east of the Great Dividing Range has also occurred in irrigated lucerne and has been partly possible because temperatures are suitable during winter. This has allowed at least five generations per year to develop, including at least two capable of causing major damage. Most farms in the Hunter dairying region now have lucerne flea present but not all experience damaging populations. Numbers on these farms tend to increase as stands age.

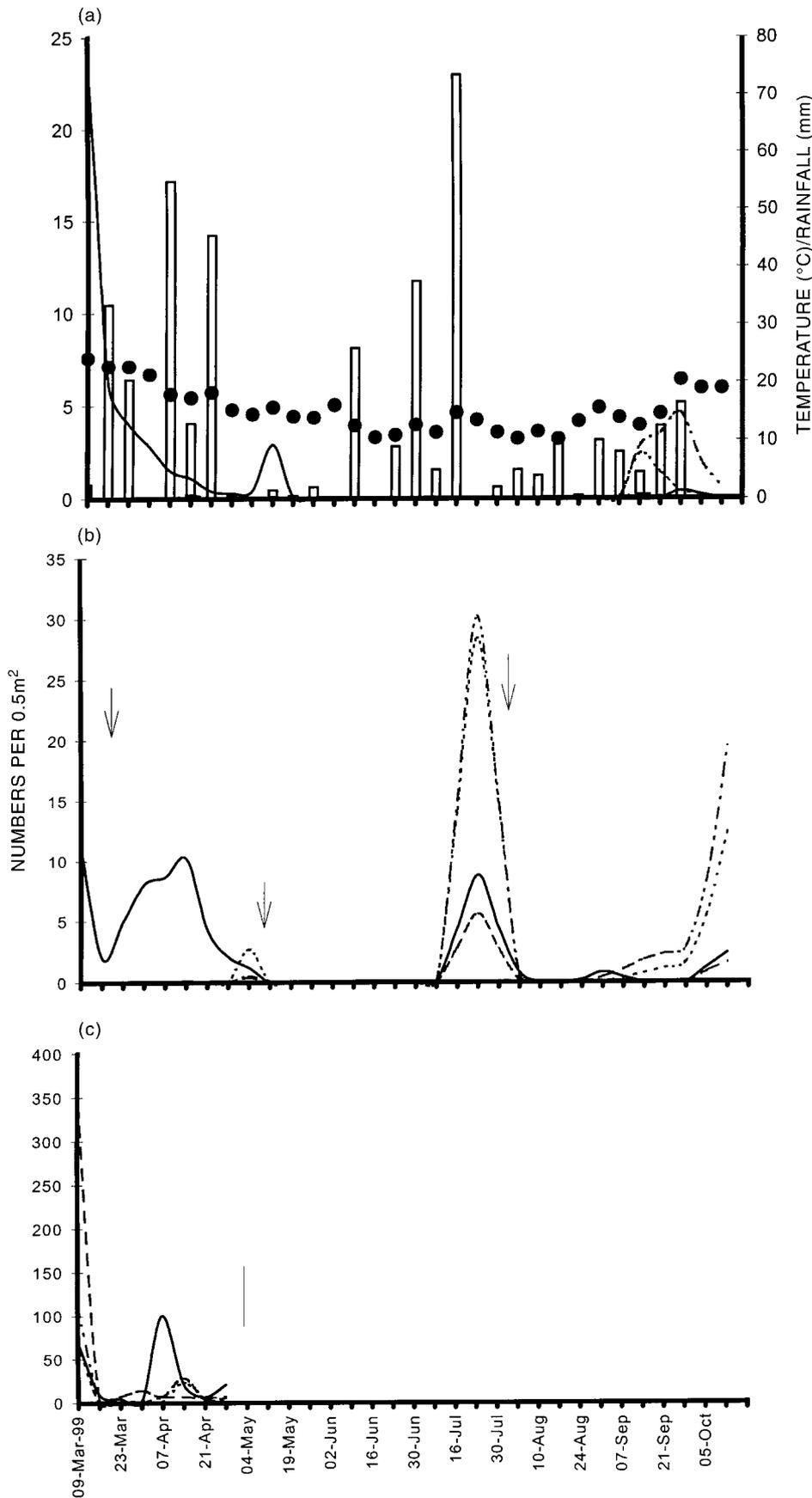
The decision that the lucerne flea could not survive beyond the limits predicted was based on the species' ability to survive hot dry summers in southern Australia. This included the production of diapause in aestivating eggs and for these eggs to respond to specific conditions under which diapause would later be broken in autumn. Areas of summer rainfall, especially when summer moisture can be augmented by irrigation, do not have distinct dry periods or the maturing of annual plants that stimulate the production of diapausing eggs. Maturing of lucerne before harvests could possibly provide some of the necessary stimuli (Wallace & Mahon 1971), although the impact could be lessened or negated by the practice of strip grazing and the growing of winter-active lucerne cultivars that would ensure the continuous availability of suitable host plants. If non-diapausing eggs predominate, any nymphs hatching should be susceptible to high summer temperatures.

Our data show that eggs hatched periodically through summer and were from the same generation of females in spring, as none developed to produce more eggs. It was not clear if, or to what degree, diapausing eggs contributed to the

start of activity in autumn, although there was some evidence of specific autumn hatchings in 1999. Understanding was confounded by hatchings leading to a new generation when temperatures averaged approximately 25°C in the absence of significant rainfall (albeit after irrigation) in autumn 1998 and by the high levels of activity at Whittingham starting well before March in 1999. It is possible that eggs hatch periodically and the nymphs die until some hatching occurs when conditions are suitable. It has been shown that non-diapausing eggs laid in spring can continue to hatch over long periods (Wallace 1968) and summer irrigation could possibly induce hatching in some diapausing eggs. These summer hatchings could deplete populations before the next season. Development after hatchings in autumn was consistent with activity expected across southern Australia with irrigation compensating for any lack of winter rainfall. Excessive rainfall and minor flooding apparently contributed to reduced population growth (e.g. July/August 1998), as described by Johnston (1960).

Pitfall traps were used in the present study in an attempt to gain better information on the association that the lucerne flea has with the ground (i.e. after hatching, to ingest soil particles and when ovipositing). The only differences between pitfall trapping and vacuum sampling (apart from the obvious and unrelatable difference in density) were: (i) the detection of very small nymphs in pitfall traps much earlier than activity was detected on plants; and (ii) the higher proportions of small and very small nymphs in these traps early in the 1997 season. These results suggested that pitfall traps could be used to alert producers or advisers of impending activity and help in the making of treatment decisions.

The two native predatory mites found in the Hunter region were not shown to be directly associated with the lucerne flea. Associations between *B. affinis* and aphids were found and have been recorded previously (Bishop & Milne 1986). The importance of spiders could be considered further. However, to be realistic, the complex would need to be differentiated by species or behavioural groups and, while spiders are possibly capable of at least functional responses to increases in flea numbers, they are unlikely to respond numerically at winter temperatures. None of the predatory species effective across southern Australia have ever been



**Fig. 2.** Distributions of numbers of different stages of the lucerne flea at three locations near Singleton in the Hunter Valley in 1999: (a) Scott's Flat; (b) Mount Thorley; (c) Whittingham. (□), Rainfall; (●), average temperature; (—), small nymphs; (---), medium nymphs; (- - -), large nymphs; (- - -), adults. Arrows on (b) indicate when spraying occurred; line on (c) indicates when sampling was terminated.

recorded in the Hunter region and insecticide use is currently the only control option for the lucerne flea.

Significant relationships were found between the lucerne flea and change in plant growth, quantifiable damage to plants and to reductions in yield. The bent-stick analysis suggested that lucerne can tolerate a level of damage after which the damage effects increase more quickly to levels possibly requiring control of the lucerne flea. This suggests that the development of treatment thresholds at or before the points at which damage increases could be feasible. Damage assessments at different stages of crop growth would be needed for any threshold to be of practical use.

With the exception of the generalised prediction of MacLagan (1932), early estimates of the limits of spread and establishment of the lucerne flea in NSW have proven to be incorrect. Irrigation appears to have contributed to this change by providing moisture when seasonal rainfall is irregular or inadequate. How the lucerne flea survives summer in the Hunter region still requires clarification. Periodic hatching, whether from diapausing or non-diapausing eggs, occurred in summer and mainly resulted in the failure of populations to develop. Mortality during summer could have a major influence on the size and viability of subsequent generations. Regardless, the species was capable of initiating viable populations in autumn and causing damage in winter. It is possible that, while the lucerne flea is still changing the limits of its distribution, it could also be adapting to different conditions under which it must survive and establish and can then cause damage.

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## REFERENCES

Bishop AL. 1991. Lucerne flea, *Sminthurus viridis* (L.) in the Hunter Valley, NSW. In: *Proceedings of a National Workshop on Redlegged Earth Mite, Lucerne Flea and Blue Oat Mite* (ed. J Ridsdill-Smith) pp. 141–147. Department of Agriculture, Western Australia, South Perth.

- Bishop AL, Holtkamp RH & Horwood M. 1991. The distribution of earth mites and lucerne flea in New South Wales. In: *Proceedings of a National Workshop on Redlegged Earth Mite, Lucerne Flea and Blue Oat Mite* (ed. J Ridsdill-Smith) pp. 20–23. Department of Agriculture, Western Australia, South Perth.
- Bishop AL, McKenzie HJ, Barchia IM & Spohr LJ. 1998. Efficacy of insecticides against the lucerne flea, *Sminthurus viridis* (L.) (Collembola: Sminthuridae), and other arthropods in lucerne. *Australian Journal of Entomology* **37**, 40–48.
- Bishop AL, McKenzie HJ, Harris AM & Barchia IM. 2001. Control strategies for the lucerne flea, *Sminthurus viridis* (L.) (Collembola: Sminthuridae), and their effect on other species in irrigated lucerne in the Hunter dairying region of New South Wales. *Australian Journal of Entomology* **40**, 79–84.
- Bishop AL & Milne WM. 1986. The impact of predators on lucerne aphids and thus on the seasonal production of lucerne in the Hunter Valley, New South Wales. *Journal of the Australian Entomological Society* **25**, 333–337.
- Davidson J. 1934. The 'Lucerne Flea' *Sminthurus viridis* L. (Collembola) in Australia. *Bulletin of the Council for Scientific and Industrial Research* No. 79.
- Holtkamp RH & Thompson JI. 1985. A lightweight self-contained insect suction sampler. *Journal of the Australian Entomological Society* **24**, 301–302.
- Johnston CJR. 1960. Biology and control of lucerne flea. *Journal of Agriculture, Victoria* **58**, 505–515.
- Launders T, Nash V, Bishop A, Nickandrow A, Richards A & Crocker G. 1997. *Maximising Dairy Production by Improved Lucerne Management in the Hunter Region*. Report on a Pilot Study for the Dairy Research and Development Corporation. NSW Agriculture, Orange.
- Lerman PM. 1980. Fitting segmented regression models by grid search. *Applied Statistics* **29**, 77–84.
- MacLagan DS. 1932. An ecological study of the 'lucerne flea' (*Sminthurus viridis* Linn.): I. *Bulletin of Entomological Research* **23**, 101–145.
- Schall R. 1991. Estimation in generalized linear models with random effects. *Biometrika* **78**, 719–727.
- Wallace MMH. 1957. Field evidence of density-governing reaction in *Sminthurus viridis* (L.). *Nature* **180**, 388–390.
- Wallace MMH. 1967. The ecology of *Sminthurus viridis* (L.) (Collembola) I. Processes influencing numbers in pastures in Western Australia. *Australian Journal of Zoology* **15**, 1173–1206.
- Wallace MMH. 1968. The ecology of *Sminthurus viridis* (Collembola) II. Diapause in the aestivating egg. *Australian Journal of Zoology* **16**, 871–883.
- Wallace MMH & Mahon JA. 1971. The ecology of *Sminthurus viridis* (Collembola) III. The influence of climate and land use on its distribution and that of an important predator *Bdellodes lapidaria* (Acari: Bdellidae). *Australian Journal of Zoology* **19**, 177–188.

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