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Predictions of summer diapause in the redlegged earth mite, *Halotydeus destructor* (Acari: Penthaleidae), in Australia

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Abstract

A prediction for the onset of a summer diapause in the eggs of the redlegged earth mite, *Halotydeus destructor*, was developed for Australia. In this species diapause eggs pass the summer in the cadavers of adult female mites. Adult female mites were collected for several weeks from pastures in spring at 18 sites in south-western Australia and dissected to determine the timing of the production of diapause eggs. Some sites were sampled for several years between 1990 and 1997. A model was developed to predict the time for onset of diapause. The week at which 90% of eggs were in diapause was predicted best by daylength (80.1% of the variability), then by duration of the long-term plant growing season (10.4%, of variability), leaving 9.5% due to other factors. A single chemical spray in spring 2 weeks before the production of 90% diapause eggs resulted in 99% fewer mites present in autumn 7–8 months later at three sites. The timing of the spring spray was the factor leading to successful control. This model was tested at 17 sites across the whole geographical distribution of the redlegged earth mite in Australia between 1998 and 2001. The observed week of 90% diapause was within 1 week of the predicted week on 81% of occasions, and 2 weeks earlier on 15% of occasions. A database was created for the predicted date of onset of 90% diapause for the whole distribution of the redlegged earth mite in southern Australia on a 10 km^2 grid. Australian farmers are using this for timing a spring spray to control mites in the following autumn.

Keywords: *Halotydeus destructor*; Embryonic diapause; Onset of diapause; Photoperiod; ANUCLIM; Australia

1. Introduction

The redlegged earth mite, *Halotydeus destructor* (Tucker) (Acari: Penthaleidae) is distributed across southern Australia in regions with a Mediterranean-type climate, consisting of cool moist winters and dry summers (Wallace and Mahon, 1971). The plants in these regions grow at lower temperatures and lower light intensity during the winter than summer-growing plants, and the length of their growing season is restricted by low rainfall in summer (Fitzpatrick and Nix, 1970). Phytophagous invertebrates feed on green plants for about 6 months, and many have a protective stage to survive the hot dry summers (soil temperature up to 50 °C). The redlegged earth mite is well adapted to this environment with a summer diapause in the eggs, which are retained in the cadaver of the female (Norris, 1950; Wallace, 1970a, b; Ridsdill-Smith and Annells, 1997). Eggs dissected from field-collected mites from May to September hatch at 16 °C in 6–10 days, but eggs collected from mid-September till late-October take 170 days to hatch (Wallace, 1970a). After some 4–6 weeks exposure to high temperatures the eggs are able to hatch in the laboratory again in a short period. This is an embryonic diapause, that is broken by exposure to high temperatures (Wallace, 1970a). In the field the

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redlegged earth mite eggs do not hatch until there is adequate soil moisture (a rainfall event) and the mean daily temperature falls below 20.5 °C for 10 days which usually occurs in the following autumn (Wallace, 1970b).

In south-western Australia *H. destructor* are active for 27 weeks from late autumn (May) till mid-spring (October), completing three generations at approximately 8-week intervals (Ridsdill-Smith and Annells, 1997). Synchronization of the generations was high in the autumn when the eggs from the summer hatched, but the generations became less synchronized during the year. The population at the peak of the first generation consisted of 65% eggs, and 14% old mites, for the second it was 49% eggs and 18% old mites, while for the third it was 24% eggs and 38% old mites (Ridsdill-Smith and Annells, 1997). By mid-October, in late spring, *H. destructor* stopped laying eggs on pasture, and the number of eggs in adult female mites increased (Ridsdill-Smith and Annells, 1997). These diapause eggs can be distinguished from winter eggs in dissected adult female *H. destructor* by their shape, size and colour (Norris, 1950).

Redlegged earth mite control in Australia has proved difficult especially in autumn, when mites emerge on different dates each year, and damage frequently occurs before it is evident that damaging populations are present. Sprays do not kill mite eggs, and when many eggs are present they hatch shortly after a control treatment. If the timing of onset of diapause could be predicted Ridsdill-Smith and Annells (1997) suggest control of the redlegged earth mite in spring to prevent the production of over-summering eggs would provide benefits both to pasture growth in spring and to plant seedling survival the following autumn. Wallace (1970a) suggests that maturation and senescence of pasture plants, and especially capeweed (*Arctotheca calendula*), has a major role in initiating diapause. However, R. Chapman (pers. comm.) showed that capeweed do not affect the onset of diapause. We describe here the geography of the onset of *H. destructor* diapause in Australia and relate it to environmental factors. A successful prediction would be the basis for a new approach to mite control.

2. Material and methods

2.1. Sampling and dissecting mites

Active redlegged earth mites were collected with vacuum samples from annual pastures using a petrol-driven garden vacuum (Ryobi Sweeper-Vac RSV 1100A MKII) sampler. The contents of the container were transferred into vials containing 70% ethanol using a sieve (0.3 mm aperture mesh) to retain the larger mites. This procedure was repeated until it was estimated there were sufficient mites to sub-sample 100 adult female redlegged earth mites.

In the laboratory, 100 mature adult female mites were differentiated (using a binocular microscope with 12 × magnification), from immature adults and large nymphs by their larger size, their bodies are blacker in colour, and more rounded in shape. White or cream genital plates distinguished females from males, which have orange or red plates (Ridsdill-Smith and Annells, 1997). Eggs were teased from the body using dissecting pins, and the diapause eggs distinguished from winter eggs by their shape, size and colour (Norris, 1950). Diapause eggs are more or less bean shaped whilst winter eggs are a symmetrical ovoid shape, on average they are larger than winter eggs, and a darker orange colour. The chorion of diapause eggs is noticeably thicker than that of winter eggs and is visible as a dark rim surrounding the egg (at 12 × magnification). The total number of winter and diapause eggs were used to estimate the percentage of diapause eggs.

2.2. Data to predict the onset of diapause

Mites were sampled from 18 annual pasture sites across the agricultural regions of south-western Australia (Fig. 1), over the period 1990–1997, but not every site was sampled every year. There were 30 sets of data. The predominant pastures species were subterranean clover (*Trifolium subterraneum*), annual ryegrass

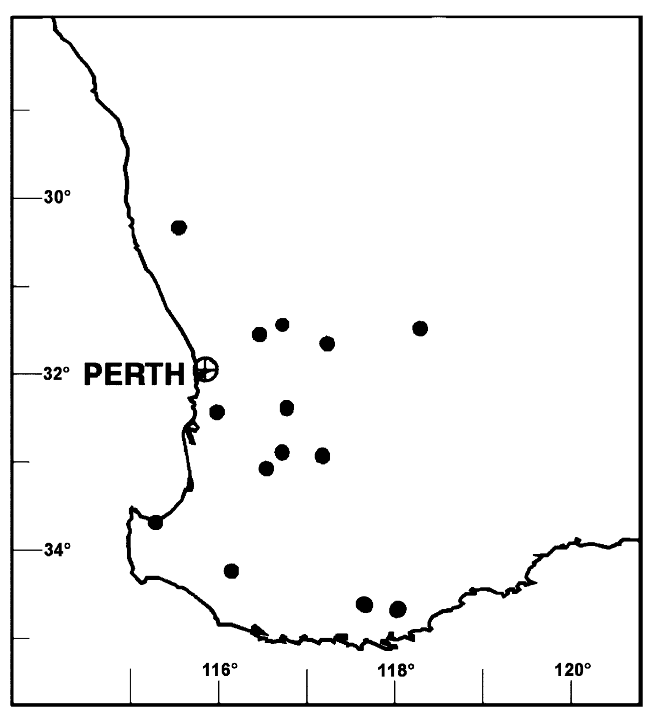

Fig. 1. Sites in Western Australia sampled to collect data for development of the diapause model.

(*Lolium rigidum*), barley grass (*Hordeum leporinum*) and capeweed (*A. calendula*). It was observed that a few pastures in any area remained green longer than the majority because of soil type, higher moisture levels, or sheltered from desiccating winds. Mites remained active for longer in these pastures, and a second site was selected at each of Cunderdin, Keysbrook, Narrogin and Busselton in 1996 (four sites), within 2 km of the original sites, to determine if pasture condition affected the onset of diapause.

Mites were sampled weekly at each site for 3 weeks before the onset of diapause, the week of appearance of diapause, and 3 weeks after, or for different periods depending on the onset of diapause, or mites dying earlier from desiccation. On average, there were eight sampling events/site/year (range 2–13 weeks), and the proportions of diapause eggs were plotted against sample week. The date on which 90% of eggs were diapause eggs was estimated from the graph (Fig. 2). Wallace (1970a) noted that the date on which the first diapause egg was observed was considerably less consistent than the date on which all eggs were diapause eggs. Both in our data and that of Wallace there were lumps in the graphs indicating that different cohorts of mites were developing diapause eggs (e.g. Toodyay, Narrogin in Fig. 2). For purposes of mite control the higher figure of 90% of eggs in diapause provided a more reliable figure to work with, although it may give less information on the mechanisms involved than the use of 10% or 50% diapause.

Environmental data were collected for 6 weeks before and 6 weeks after the 90% egg diapause date in order to find which factor provided the best prediction for onset of diapause. In spring in southern Australia temperatures and daylength increase, and rainfall decreases. Changes in all these factors could influence the production of diapause eggs. For each site mean weekly rainfall, minimum temperature and maximum temperature was obtained from the nearest meteorological station (Australian Bureau of Meteorology) for the 13-week sampling period.

Daylength (minutes) is taken to be the time between when the sun rises above and when it drops below the horizon, ignoring twilight, and was obtained from Geoscience Australia (http://www.ga.gov.au/nmd/geodesy/astro/sunrise.jsp). In Australia the mites occur in winter

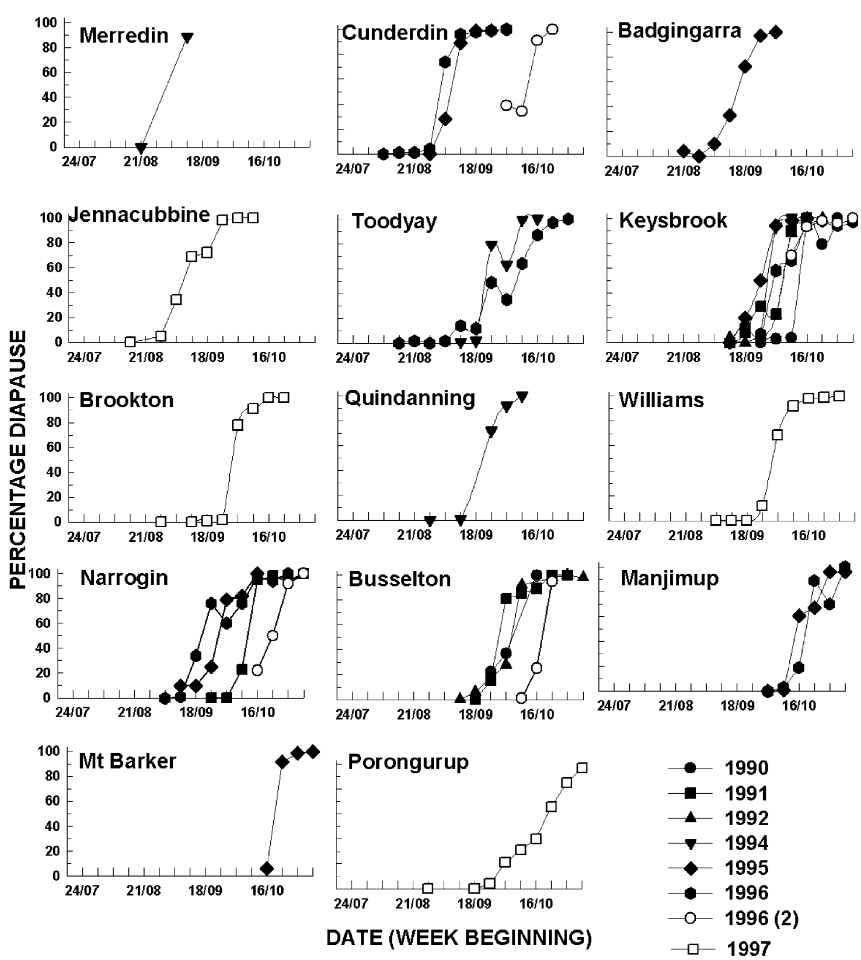

Fig. 2. Development of diapause eggs at sites in south-western Australia from 1990 to 1997.

rainfall areas from 28°00′ to 43°20′S and 114°10′ to 150°50′E (Ridsdill-Smith, 1997). The annual range of daylengths at the latitudes where *H. destructor* occurs in Australia varies from 3 h 32 min to 6 h 25 min (Fig. 3). The lengths of day and night are equal (12 h) between weeks 12 and 13 in autumn and weeks 41 and 42 in spring.

Factors that varied between sites but not between weeks were also considered in the prediction of onset of diapause. They were annual rainfall, and duration of growing season. In winter–rainfall regions a quick estimate of length of growing season can be made from monthly data on temperature and rainfall. The mean monthly temperature [(min temperature + max temperature)/2] is plotted against mean monthly rainfall in the ratio 10 °C : 20 mm (Fig. 4). The growing season is the period over which the plot for rainfall is above the plot for temperature (Walter and Leith, 1967). This was estimated for each site both for the year of sampling (growing season of year), and for long-term average data (long-term growing season).

2.3. Using a single spring spray to control redlegged earth mite in autumn

Pastures containing redlegged earth mite were sprayed in spring 1997 at three sites 2 weeks before the onset of 90% diapause to determine if this controlled mites emerging the following autumn. Spray dates were 2 weeks before the occurrence of 90% diapause at each site, when it was expected that few diapause eggs would have been produced. Dates were estimated from 1990 to 1996 measures of occurrence of 90% diapause eggs in the region (Fig. 2). The sites were at Brookton (32°24′S, 116°46′E, 462 mm annual rainfall), Williams (32°54′S, 116°43′E, 550 mm annual rainfall), and Porongurup (34°41′S, 118°0′E, 650 mm annual rainfall) in south-western Australia. At each site a pasture area of at least 4 ha was selected, one half of which was left unsprayed as the control, and the other half was sprayed by the farmer with his own equipment. The farmer used organo-phosphates at the recommended label rate, on the spray date predicted. At Brookton, omethoate was sprayed at 100 ml/ha on 11 September, at Williams, omethoate was applied at 100 ml/ha on 18 September, and at Porongurup, dimethoate was sprayed at 200 ml/ha on 11 October (higher rate for tall pasture).

Redlegged earth mite abundance was measured with 20 samples from the unsprayed area and 20 from the sprayed area at each site, taken on a transect through the centre of each 2 ha area at about 10 pace intervals. Each sample (109 cm^2) was obtained with a 5 s suck with the petrol driven garden vacuum. Mean number of mites/core provided a measure of their relative abundance.

2.4. Model fitting

One date of 90% diapause was observed from the dissections for each site and year when samples were taken (26 sets of data from 14 sites) over the period 1990–1996 (Fig. 2). A multiple linear regression model was used to determine the relation between time and the environmental data, where time was denoted as negative for 6 weeks before 90% diapause, zero at week 0 (the 90% diapause week), and positive for the 6 weeks after 90% diapause eggs were produced. Because the coverage over locations by years was incomplete, a multi-linear regression approach with forward selection was used to identify the relative importance of the factors in

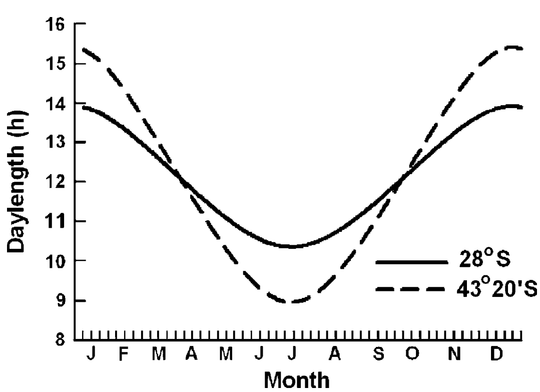

Fig. 3. Daylengths for latitudes at the northern and southern limits to redlegged earth mite distribution in Australia (algorithm in Sands and Hughes, 1976).

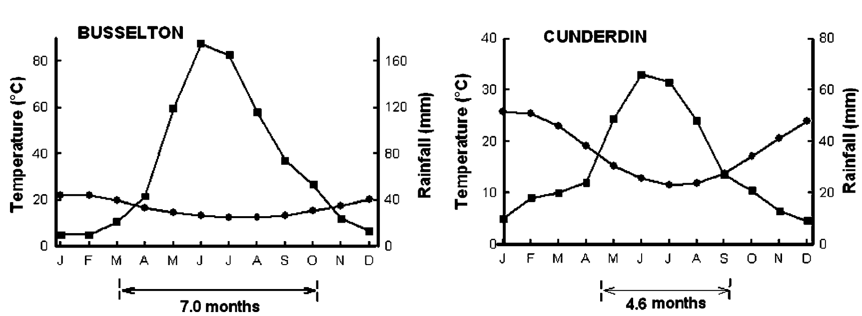

Fig. 4. The length of two contrasting growing seasons (Busselton and Cunderdin, Western Australia) estimated from temperature (circles) and rainfall (squares) (method in Walter and Leith, 1967).

predicting time (week 0) using GENSTAT (General Statistical Package—from Lawes Agricultural Trust, Rothamsted Experimental Station, UK). The residual mean square (RMS) on fitting a constant to all the data was 13.81 ($n = 338$). The best single factor to predict time was daylength (in minutes) which reduced the RMS to 2.70 (80% of variance was accounted for by constant plus daylength) (Table 1). The improvement in fit by taking the constant plus daylength and adding each of the other factors in turn is given in Table 1. Those producing the best fit (lowest RMS) were group (site × year) and site, but these were unique and neither would aid in predicting diapause generally. The next most important factor was the long-term growing season which reduced the RMS to 1.39 (90% of variance was accounted for by daylength plus long-term growing season). None of the other factors provided an improvement in the prediction of week 0 to the regression of constant plus daylength over that with long-term growing season (Table 1). Omitting the extra locations (Cunderdin 2, Keysbrook 2, Narrogin 2, Busselton 2 in Table 3) selected to test variability in diapause in a locality did not change the conclusions and the more robust model was retained. (Table 1).

The selected model was fitted to the full data set from 1990 to 1997: $c(0) + c(1)$ (daylength) $+ c(2)$ (long term growing season) ($n = 374$) (13 weeks for 30 sets of data, 18 sites over some of 7 years) (Table 2). The model accounted for 90.4% of the percentage variance. The fitted equation was:

$$Y = -44.487 + 0.06487\ (\text{daylength}) - 1.1163\ (\text{long-term growing season}).$$

Since week 0 (where $Y = 0$) was coded as the week 90% of the eggs were found to be diapause eggs, the fitted equation can be transformed to predict daylength for the date on which 90% diapause has occurred. That is:

$$\text{Daylength} = [(Y = 0) + 44.487 + 1.1163\ (\text{long-term growing season})]/0.06487.$$

The daylengths are converted back to dates (using the algorithm), which are expressed as weeks using the Julian calendar (http://www.control.auc.dk/~tb/temp/java/Calendar.html).

2.5. *Mapping distribution of dates for onset of diapause across Australia*

Maps were developed to extend the model developed for sites in south-western Australia to the rest of the distribution of *H. destructor* in Australia. Daylength was calculated with an algorithm using latitudes and longitudes (Sands and Hughes, 1976). Long-term growing season for points over southern Australia was obtained from average weather data (Walter and Leith, 1967).

Table 1
Sequence of best environmental predictors of the week in which 90% diapause eggs occurred for data from south Western Australia 1990–1996

Factor	RMS (all data)	RMS (without extra sites)[a]	Regression
Constant	13.81	13.77	C
Daylength	2.70	2.77	C + D
Group (site × year)	0.04	0.04	C + D + group
Site	0.51	0.59	C + D + site
Long term growing season	1.39	1.00	C + D + long growing season
Growing season of year	1.85	1.79	C + D + growing season
Annual rainfall	1.99	1.94	C + D + annual rain
Maximum weekly temperature	2.10	2.08	C + D + max weekly temp
Year	2.50	2.59	C + D + year
Weekly rainfall	2.58	2.65	C + D + weekly rain
Minimum weekly temperature	2.70	2.78	C + D + min weekly temp

RMS = residual mean square.
[a]A second site was selected at four locations where pasture stayed green for longer in the spring to determine the effect on onset of diapause. These extra sites are excluded from the regression here to determine how much the RMS changed.

Table 2
Analysis of variance predicting time (containing week of production of 90% diapause eggs)

Change	Df	Sums of squares	Residual mean square	Variance ratio	*P*
+ Daylength	1	4065.1	4065.1	3117.5	0.001
+ Long-term growing season	1	526.1	526.1	403.5	0.001
Residual	370	482.5	1.304		
Total	372	5073.7	13.639		

Meteorological data for the maps was derived from ANUCLIM 1.6 (Houlder et al., 1998). The maps were developed using Arc/Info version 6.0 (ESRI, www.esri.com, Redlands California), firstly by generating a regular geographic fishnet with a mesh size of 0.1 arc degrees. The centroids of the gap polygons were then established, and the elevation at each of the centroids was estimated using the 1/40th degree digital elevation model (Australian National University) within Arc/Info. The centroid locations and their estimated elevations were then used to extract the relevant meteorological variables from ANUCLIM 1.6 (Houlder et al., 1998). A FORTRAN 77 program was developed to apply the following rules to the extracted meteorological database for each grid point, and to calculate the appropriate onset of diapause date (Ms. Anne Bourne, CSIRO Entomology, unpublished data). The algorithms (rules) used to describe mite distribution are that it is: (a) to be within the 205 mm rainfall isohyet for the growing season (May–October); (b) to be outside the 225 mm isohyet for midsummer rainfall (December–March) and: (c) to be outside the area where mean monthly maximum temperature of the hottest month (usually January) is below 33 °C, and where there is some summer rain (Wallace and Mahon, 1971).

Dates for onset of diapause produced from the algorithms for daylength and long-term growing season were converted to weeks and plotted using the fishnet polygon coverage to create a prediction for the whole area at approximately 10 km scale. Co-ordinate data on place names were sourced from Geoscience Australia Place Name website (http://www.ga.gov.au/map/names/). The database could then be searched by latitudes and longitudes or by place names to obtain the date of onset of diapause.

2.6. Model validation

To validate the model a further 27 sets of data were collected from 17 sites between 1998 and 2001 across southern Australia (Fig. 5). At the eastern edge of *H. destructor* distribution in Australia where more summer rain occurred, the Walter and Leith algorithm did not provide an estimate of the long-term growing season. A number of alternative approaches were made to calculate the length of growing season. These included trying to fit the Fitzpatrick and Nix (1970) model of growth indices (see Sands and Hughes, 1976). The results (not given here) proved unsuccessful probably because of variability in soil type and altitude. To make the database complete for Australia a further 30 sets of data were collected from this region of New South Wales, Victoria and Tasmania, from 20 sites between 2000 and 2002. Dates when 90% diapause occurred were mapped, and the predicted dates determined by visual extrapolation to the whole area.

3. Results

3.1. Data to predict the onset of diapause

The date on which 90% of eggs were diapause eggs in south-western Australia varied from week 39 to 44 of the year (September, October) (Table 3). At the extra sites where the pasture remained green for longer (the site 2 s in Table 3) the week on which 90% diapause occurred was usually 1 or 2 weeks later than the nearby pasture in the same location. At Cunderdin site 2 it was 5 weeks later, a much larger difference than expected, which remains unexplained.

3.2. Control of the redlegged earth mite with a spring spray

Abundance of mites was high in both treated and control areas in the pre-spray sample, 2 days before spraying (average 386 mites/core) (Table 4). The spray was effective in killing all active mites (average 2.7 mites/core), with 99% fewer mites in the sprayed than

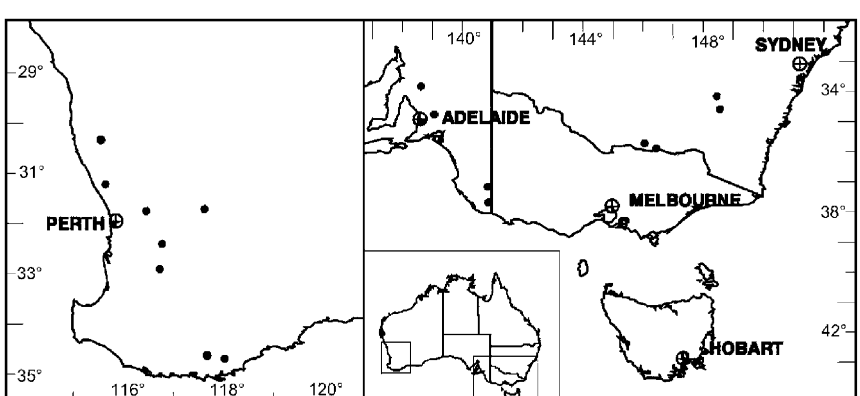

Fig. 5. Sites where independent data for the onset of diapause were collected to validate the model in southern Australia.

Table 3
Observed date of 90% diapause for sites in Western Australia used for developing model

Site	Week in which 90% diapause was observed						
	1990	1991	1992	1994	1995	1996	1997
Merredin	—	—	—	37	—	—	—
Cunderdin	—	—	—	—	37	37	—
Cunderdin 2	—	—	—	—	—	42	—
Badgingarra	—	—	—	—	39	—	—
Jennacubbine	—	—	—	—	—	—	39
Toodyay	—	—	—	40	—	41	—
Keysbrook	43	41	42	40	39	41	—
Keysbrook 2	—	—	—	—	—	42	—
Brookton	—	—	—	—	—	—	40
Quindanning	—	—	—	39	—	—	—
Williams	—	—	—	—	—	—	41
Narrogin	—	41	—	—	41	41	—
Narrogin 2	—	—	—	—	—	43	—
Busselton	—	—	—	42	43	41	—
Busselton 2	—	—	—	—	—	43	—
Manjimup	—	—	—	—	42	43	—
Mount Barker	—	—	—	—	43	—	—
Porongurup	—	—	—	—	—	—	44

Table 4
A single spring spray used to control the redlegged earth mite over summer in south Western Australia, 1997–1998

Site	Treatment	Spray date	Mites/core (±se)		
			Pre-spray	Post-spray	Autumn
Brookton		11 Sept	9 Sept	16 Sept	21 May
	Spray		197±13	3±0.5	0.5±0.3
	Control		232±25	371±25	167±59
Williams		18 Sept	16 Sept	23 Sept	29 April
	Spray		492±25	3±0.7	0.1±0.1
	Control		570±49	623±33	537±80
Porongurup		11 Oct	8 Oct	15 Oct	28 April
	Spray		441±34	2±0.4	4±0.8
	Control		382±26	619±47	172±20

unsprayed area on average 2 weeks after the spray. On the spray date (2 weeks before the 90% diapause) dissections of mites showed no diapause eggs at Brookton and Williams, but 33% at Porongurup. In the following autumn 7–8 months after the single spray, mite control was over 99% at Brookton and Williams (average 0.3 mites/core), and 97.7% at Porongurup (average 4 mites/core) (Table 4). Interestingly the presence of nearly one third of diapause eggs at Porongurup in spring at the time of spraying did not result in a proportionally reduced level of mite control the following autumn.

3.3. Model validation

Occurrence of the week when 90% of eggs were in diapause was observed for 27 sites across southern Australia as independent tests of the model (Table 5). Other sites where sampling was started, the dates could not be obtained because adult mites died when the season ended early, or critical samples were lost. At 81% of sites the observed week was within 1 week of the predicted, at 15% it was within 2 weeks and these observed weeks were all earlier than the predicted. At one site (4%), Naracoorte, the observed was 3 weeks later than the predicted in 1998.

A further 30 sets of data were obtained from sites with greater summer rainfall on the eastern edge of *H. destructor* distribution in Australia, where the model could not be used (Table 6). Here the predicted dates were obtained by plotting up the observed weeks on a map and estimating the predicted weeks by eye. No model was used. The results were a bit more variable than for the regions where the model did work. At 67% of the sites the observed week was within 1 week of the predicted, at 27% of sites they were within 2 weeks of predicted and at one site it was within 4 weeks (3%) and at one site within 5 weeks (3%).

3.4. Database for onset of diapause for H. destructor in Australia

An Excel database was set up containing the outputs of the model, and a date of 90% diapause calculated for every 10 km^2. The information on the date of 90% diapause can be retrieved by searching latitudes and longitudes for any locality where *H. destructor* is found.

Table 5
Observed and predicted dates of 90% diapause from independent test sites

Site	Week of 90% diapause				
	Predicted	1998	1999	2000	2001
Cunderdin	38	39	39	—	—
Badgingarra (1)	40	—	39	—	—
Badgingarra (2)	40	—	—	—	40
Gingin	41	—	—	—	40
Bakers Hill	41	—	—	—	40
Brookton	40	41	—	—	—
Williams	41	41	40	—	—
Mount Barker	43	—	—	41	—
Porongurup	43	43	41	41	—
Clare	41	42	—	—	—
Mount Pleasant	43	43	—	—	—
Naracoorte	42	45	41	—	—
Mount Gambier	44	45	43	—	—
Bendick Murrell	43	43	42	—	—
Galong	43	44	44	—	—
Balldale	42	43	40	—	—
Savernake	41	41	40	—	—

Table 6
Measured and predicted weeks in which 90% diapause occurred for higher rainfall areas in eastern Australia

Site	Year	Latitude (S)	Longitude (E)	Week of 90% diapause	
				Predicted	Measured
Wellington	00–01	32°46′	149°01′	43	44, 44
Gooloogong	00–01	33°36′	148°26′	43	45, 44
Yass	00–01	34°50′	149°01′	43	48, 45
Gunning	00	34°50′	149°15′	43	44
Collector	00–01	34°54′	149°33′	43	45, 44
Orange	02	33°17′	149°09′	43	43
Kendall (1)	01	N/A	N/A	43	45
Kendall (2)	01	N/A	N/A	43	41
Tumut	00–01	35°21′	148°17′	43	43, 45
Tallangatta	00–02	36°13′	147°10′	44	43, 44
Millthorpe	00	33°26′	149°11′	43	47
Kilmore	00	37°17′	144°57′	44	44
Rosewhite	00	36°35′	146°52′	44	43
Carlisle River	00	38°31′	143°20′	44	44
Kergunyah	02	36°20′	147°02′	43	43
Oatlands	00 & 02	42°18′	147°22′	43	44, 44
Ross	00 & 02	42°01′	147°29′	43	44, 44
Sorell	00 & 02	42°47′	147°33′	43	43, 43
Cressy	00 & 02	41°40′	147°04′	43	45, 43
Pipers River	00	41°05′	147°04′	44	46

A gazetteer using the Geoscience Australia Place Name website was also added to give names that could be used to locate a site. Spray dates in the database are exactly 2 weeks before the date of 90% diapause.

4. Discussion

For the mite *H. destructor* the onset of diapause in spring was predicted by daylength and the duration of long-term plant growing season over an area of Australia of some 1700 km × 3300 km. *H. destructor* occurs only in areas with Mediterranean-type climates in South Africa, Australia and New Zealand. It is very abundant in Australia, and summer diapause is one factor allowing the mites to thrive in this environment. The mites are metabolically active during the shorter days and lower temperatures of winter, while in spring the adult female produces diapause eggs and dies. In spring we have shown in this paper that the onset of diapause occurs at each site at much the same time in different years. However, mites may remain active for a period after the diapause eggs are produced depending on the weather, and the length of this period varies between years (Ridsdill-Smith and Annells, 1997). The summer is passed in the cadaver of the maternal body. *H. destructor* emerges from the eggs in autumn at different times each year in response to local rainfall and temperature events. As a result of these mechanisms the mites avoid emerging following summer rainfall events when conditions are unsuitable for their survival, but their emergence is usually synchronized with the establishment of seedlings of the annual crop and pasture plants that provide their food. This is when severe damage to the plants occurs.

H. destructor is multi-voltine completing three generations a year in pasture in south-western Australia (Ridsdill-Smith and Annells, 1997). Only the generation present in spring produces diapause eggs. When *H. destructor* is field-collected in winter and early spring (July, August or September), and reared in the laboratory on vetch plants (*Vicia sativa*) under winter conditions (a fluctuating 11–18 °C and 10 h light:14 h dark), they continued to produce winter eggs with no evidence of any diapause eggs from August to April (Ridsdill-Smith and Gaull, 1995). While diapause responses are genetically based, environmental conditions will determine whether or not the diapause stage is developed (Tauber et al., 1986).

Most insects and mites respond to absolute photoperiods to induce diapause (Danks, 1987). The production of 90% diapause eggs in *H. destructor* occurred between weeks 37 and 44 in Australia. Daylength accounted for 80% of the observed variability and duration of long-term growing season a further 10%. Saunders (2002) gave similar figures for the variation in photoperiodic traits in geographical clines on insects. Bradshaw (1976) showed that latitude accounts for 80.5% of the variation in critical photoperiod and altitude 15.5%, for a mosquito. Altitude is an index for the duration of 'growing season' for this winter-diapause species. In the summer-diapause species, *H. destructor,* there was a positive linear correlation between photoperiod and the duration of the long-term growing season. Diapause occurred at greater daylength at sites where the duration of growing season was greater.

The cues for onset of diapause in *H. destructor* are presumably mainly detected through daylength and duration of growing season. Day and night are about equal at weeks 41 and 42 (spring equinox), at the northern and southern limits of redlegged earth mite distribution in Australia (28–43°S). However, while the daylength is getting shorter by about 20 min every week at the southern limit, it is 11 min every week at the northern limit. The rate of change of daylength length would be a less useful trait than the absolute daylength as a cue for diapause. While daylength can presumably be detected directly by the mites, the detection of changes in duration of the long-term growing season will probably be indirect. At the four greener sites in 1996 the mites usually produced diapause eggs 1–2 weeks later than more average sites in the locality. For the same daylength the mites therefore produced diapause eggs later if the plants were green rather than senescing. This may be the mechanism by which the growing season can have an indirect effect on the onset of diapause. Wallace (1970a) believed that food plant maturity (quality) was the primary factor affecting onset of diapause in *H. destructor*. However, the relationship was greater with the long-term average growing season than the growing season of the year. This would occur if the growing season was perhaps changing sensitivity to photoperiod, rather than the food acting directly on the mites. In many phytophagous insect species diapause induction is modified by the status of the food plant, such as senescence of plants at the end of the growing season (Danks, 1987; Veerman, 1992; Saunders, 2002).

H. destructor populations are not well synchronized in spring; at the peak of the third generation at Keysbrook 38% of the population on average were old mites (Ridsdill-Smith and Annells, 1997). Diapause eggs developed in mature adult female mites. Once the environmental conditions that resulted in the production of diapause eggs occurred in spring, the diapause eggs appeared as the different cohorts of mites completed their development to adult. This was evident both in our data and those of Wallace (1970a) where there were peaks in the curve of increasing proportion of *H. destructor* diapause eggs over time.

The window of sensitivity to photoperiod is usually fairly brief (Denlinger, 2002). This usually occurs during the development stage prior to the stage in which diapause is expressed (Veerman, 1992), and frequently this is in the maternal generation (Danks, 1987; Saunders, 2002). *H. destructor* development from egg to adult takes 27–31 days, and adults can live for 25–56 days (Ridsdill-Smith, 1997). The mites do not accumulate more than 10 eggs/mite before oviposition during the winter, and it is likely that as eggs are laid more are developed. The average complement of about 40 diapause eggs/mite are probably also produced over time (Ridsdill-Smith and Annells, 1997). Experimental data would be required to establish which *H. destructor* stage was sensitive to photoperiodic changes.

This model of onset of diapause is being widely used in a control package for *H. destructor*. A single organophosphate spray is applied 2 weeks before the production of 90% diapause eggs. In preliminary trials at three sites in south-western Australia in spring 1997, mite control was 98–99% in the following autumn, 7–8 months following a single spring spray at a critical time. The spring spray almost completely prevented the production of over-summering eggs. At two of the sites there were no diapause eggs present at the time of the spring spray. At the third, at Porongurup, 33% of eggs were diapause eggs at the time of the spring spray, and control the following autumn was still 98%, suggesting that newly formed diapause eggs were killed by the spray, along with the female mites. The preparative stage of diapause may involve the deposition of extra layers of hydrocarbons for waterproofing the cuticle (Denlinger, 2002). Perhaps the diapause eggs do not become fully resistant to spray until all are developed. The package TIMERITE® (www.timerite.com.au) which recommends spraying 2 weeks before 90% diapause, is being used with great success by farmers to control redlegged earth mite. Farmers obtain the optimal spring spray date by providing the locality (latitude and longitude) for the site they wish to treat and the TIMERITE® database provides the date. The database covers the whole distribution of *H. destructor* in Australia. This new approach to redlegged earth mite control, by spraying at the right time in spring, has given farmers much greater confidence in obtaining benefits from mite control than they achieved before. Over 2500 dates have been obtained by farmers from the TIMERITE® website in less than 1 year, providing benefits of many tens of millions of dollars.

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