Seasonal occurrence and abundance of redlegged earth mite *Halotydeus destructor* (Acari: Penthaleidae) in annual pastures of southwestern Australia

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Abstract

Seasonal occurrence and abundance of redlegged earth mite, *Halotydeus destructor* (Tucker), was measured by weekly sampling in grazed annual pastures near Keysbrook (1990–1992) and Narrogin (1991–1992) in southwestern Australia. Mites were active for 27 weeks from the late autumn (May) to mid-spring (October), completing three generations at approximately 8 week intervals. The summer is spent as diapause eggs in the cadavers of adult female mites. In 1991 and 1992, active *H. destructor* was on average twice as abundant at Keysbrook (mean 11,300 mites/m^2), as at Narrogin (mean 6400 mites/m^2). Three times more eggs were laid at Keysbrook than Narrogin (mean 8500 and 2900 eggs/m^2 respectively). Rainfall at Keysbrook was twice that at Narrogin, and temperatures were higher. We suggest that the rate of oviposition was less at Narrogin, probably because of resource limitation. The mature adult sex ratio was female biased, but was lower at Keysbrook (0.669) than at Narrogin (0.813). *Neozygites acaridis*, a fungal disease, was detected in less than 4% of the population, mainly in adult mites in late spring. Rainfall and temperatures were lower in the spring of 1992 than 1991 at both sites. Pasture was grazed considerably shorter in the spring of 1992, and numbers of *H. destructor* were lower, but numbers of eggs laid in the two years were similar. We suggest that active mite mortality was greater in spring of 1992, probably due to lower relative humidity. There were fewer adult mites in spring, and fewer diapausing eggs in summer at both sites in 1992 (36,600 diapause eggs/m^2) than in 1991 (148,000 diapause eggs/m^2). It is proposed that controlling mites in spring should lead to lower numbers of diapause eggs in summer and of mites emerging in autumn.

Introduction

Redlegged earth mite, *Halotydeus destructor* (Tucker) (Acari: Penthaleidae), which was accidentally introduced to Australia from South Africa in 1917, was considered a serious pasture pest throughout southern agricultural regions by 1934 (Swan, 1934), and it remains so (Panetta *et al.*, 1993). Mite feeding on pasture legumes causes seedling mortality, reduced pasture productivity and reduced seed yield (Norris, 1944; Wallace & Mahon, 1963; Brennan & Grimm, 1992). *Halotydeus destructor* is phytophagous, and will feed on nearly all agricultural and non-agricultural plants (Swan, 1934). Rates of reproduction vary greatly on the host species on which *H. destructor* can successfully breed (Annells & Ridsdill-Smith, 1994). However, on some crop species which are damaged, *H. destructor* is unable to maintain populations (McDonald *et al.*, 1995).

Halotydeus destructor occurs mainly in regions with a cool wet winter where the winter rainfall, between May and October, is greater than 204 mm, and a warm dry summer where the summer rainfall, between December and April, is

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less than 104 mm (Wallace & Mahon, 1971). *Halotydeus destructor* is active during the cooler, wetter period of the year from May to October. In spring, the female mites retain eggs in their bodies, die on the soil surface, and summer is passed as diapausing eggs (Wallace, 1970a). Diapause is broken by high temperatures, requiring an equivalent of a month with soil temperatures over 50°C (Wallace, 1970a). In autumn, the eggs hatch with adequate soil moisture, when the mean daily temperature falls below 20.5°C for 10 days (Wallace, 1970b). Survival of diapause eggs during the summer is reduced by moisture (summer rainfall) (Annells & Ridsdill-Smith, 1991), particularly in heavier textured soil (James & O'Malley, 1992). *Halotydeus destructor* appears to thrive at sites with well-drained sandy soil (Norris, 1938).

In a study of *H. destructor* abundance near Perth, Western Australia, Norris (1938) suggests that there are three generations a year, with peaks in autumn and/or spring, but the limiting factors were not detected. The aim of this paper is to provide a quantitative description of the factors affecting seasonal occurrence and abundance of *H. destructor* in grazed annual *Trifolium subterraneum* (subterranean clover = subclover) pastures, as a basis for planning better management and control of this pest. At two sites in southwestern Australia, active stages and eggs were counted during winter and spring, and diapausing eggs were counted during the summer.

Materials and methods

Description of pasture sites

Mites of *Halotydeus destructor* were sampled at two grazed pasture sites in southwestern Australia. At the site near Keysbrook (32°26'S, 115°56'E) 60 km south of Perth, mites were sampled for three years (1990–1992) in permanent pasture grazed by cattle. The long-term mean temperature for the hottest month (February) was 24.1°C and for the coldest month (July) was 13.7°C (Mandurah meteorology station), and annual rainfall was 884 mm. At the second site near Narrogin (32°56'S, 117°03'E) 180 km south east of Perth, mites were sampled for two years (1991–1992) in pasture grazed by sheep. Pasture was grown in rotation with wheat. The long-term mean temperature for the hottest month (January) was 22.7°C and for the coldest month (July) was 10.2°C (Narrogin meteorology station), and annual rainfall was 506 mm. Subsidiary sampling for disease in mites was carried out at a third site near Toodyay (31°33'S, 116°28'E), 84 km north east of Perth, on pasture grazed by cattle. The long term mean temperature for the hottest month (January) was 25.9°C and for the coldest month (July) was 11.3°C (Northam meteorology station), and annual rainfall was 433 mm. During this study, current rainfall was measured from the farm at the sampling site, and daily maximum and minimum screen temperatures from the nearest meteorology station.

The soil at the Keysbrook site was a bleached sand with subsoil pans (CD1, Plumb, 1980; based on the Northcote system). The main pasture legume was subclover cv. Dinninup, which was seeded in 1982 at 10 kg/ha. The grasses were *Lolium rigidum* (annual ryegrass) and *Romulea rosea* var. *australis* (guildford grass), while the main weed was *Arctotheca calendula* (capeweed) with lower numbers of *Erodium* spp. (storksbill) and *Hypochoeris* spp. (flatweed/cats ears). The soil at the Narrogin site was a grey/brown sand loam with clay subsoil (duplex, A2, Plumb, 1980). The dominant pasture species was subclover cv. Dalkeith, which was seeded in 1987 at 20 kg/ha (some cv. Dwalgenup was present from earlier sowing). Grasses present were annual ryegrass, guildford grass and *Hordeum leporinum* (barley grass). The weeds were capeweed, storksbill, *Rumex pulcher* (fiddle dock) and *Salvia reflexa* (mintweed). The soil at the Toodyay site was a red duplex soil without subsurface bleaching (A2, Plumb, 1980). The dominant pasture species was subclover cv. Trikkala, with some of cvs. Seaton Park and Junee. Other pasture species included capeweed, annual ryegrass and barley grass.

A visual estimate of pasture composition was made monthly from May until October each year. One operator threw a 40×40 cm quadrat onto the pasture five times inside each of 10 permanent sampling plots (50 quadrats) (see below for plot design). Estimates were made of the proportion of ground covered by subclover, capeweed, grasses, other plant species, and that which was bare. Weekly observations on the median pasture height provided an index of biomass, resulting from interactions between pasture growth and grazing intensity. Stock was rotated between paddocks. Grazing intensity was quantified at Keysbrook for cattle, and at Narrogin for sheep, from the proportion of sampling occasions each year that grazing animals were present in the field where mites were being sampled.

Sampling active mites in winter and spring

Active mites on the soil surface and foliage were sampled with a steel corer 10 cm in diameter (78.5 cm^2) (Wallace, 1956). A core 2–5 cm deep was removed, and the corer inverted over a funnel and tapped, causing the mites to fall into a collecting tube containing 70% alcohol. One hundred samples were taken weekly at each site throughout the winter (May–August) and spring (September–October) when mites were active. At each site, 10 plots of 31×6 m were marked with permanent pegs in an area of 67×38 m. The plots were in two rows of five; a gap of 2 m separated plots and 5 m separated the two rows. Within each plot there were 30 positions at 1 m intervals and, each week, one position was selected randomly; the initial point was changed each year. We did not sample adjacent positions in consecutive weeks so that we did not have interference through trampling. At the sampling position, 10 cores were taken at 60 cm intervals and starting 30 cm from the end. Core positions were found from knots in a 6 m string.

When the first substantial winter rains were expected, the sites were visited weekly and inspected for mites. Full sampling started once mites were observed. At Keysbrook in 1991 and 1992, and Narrogin in 1991, zero counts were observed for two or more weeks. At Keysbrook in 1990, there were reasonable numbers of mites and some eggs at the first sample and the start of the season was missed, probably by two weeks. At Narrogin in 1992, mites but no eggs were present at the first sample and the start of the season was missed, probably by one week. Egg-laying started after mite emergence, and sampling was continued until egg-laying ceased and until no active mites were collected in the 100 samples. The first and last week when an average of one or more mites was sampled per core represented the period of mite activity in the pasture.

Halotydeus destructor was separated under a binocular microscope into larvae (three pairs of legs), protonymphs, deutonymphs, tritonymphs and adults (four pairs of legs), and counted. Stages were separated by their relative size within each sample, to allow for environmental effects of size. The bodies of adults were blacker in colour than the nymphs, and more rounded in shape. A sample of each stage was checked by Dr A.S. Baker, The Natural History Museum, London. All adults were sexed each week; the genital plates of females are creamy or white while those of the males are orange or red. The proportion of females in the adult mite population was calculated. To investigate factors affecting oviposition, mature adult female mites were dissected. In preliminary studies, smaller adult females contained few or no developed eggs, but after feeding they were larger and contained more developed eggs. Mature females were separated from immature females on the basis of their relatively larger size. The number of developed eggs or diapause eggs/mite was counted weekly from a subsample of 50 mature female mites (five from the total in each plot). In 1992, eggs were also counted from a subsample of 50 immature adult female mites. The presence of diapause eggs inside adult female mites could be readily determined by their shape and colour. Diapause eggs were virtually bean-shaped, noticeably larger than winter eggs, and the chorion was thicker and could often be seen as a dark ring around the egg.

Disease

In 1990, some mites were found which were discoloured, and much paler. A fungal pathogen was tentatively identified by Dr R. Milner (CSIRO Entomology, Canberra) as *Neozygites acaridis* (Petch) (Entomophthorales) (Milner, 1985). In 1991 and 1992, mites showing evidence of disease were counted and the mite stage infected was recorded.

In a laboratory culture, a sticky white fungal webbing on the soil surface trapped and killed many mites (Ridsdill-Smith & Gaull, 1995). The fungus was identified as a *Verticillium* sp. and was cultivated on live mites (G. Hardy, personal communication). To see if this fungus was a significant mortality factor in the field, mites were collected five times during the winter of 1993 from a pasture at Toodyay. Ten *H. destructor* of each stage (except larvae) were washed in distilled water and 10 were surface-sterilized in sodium hypochlorite for 30 sec. Whole mites from both treatments were plated out on potato dextrose agar (PDA) incorporating streptomycin in the laboratory. The plates were incubated for one week at 22°C and >95% relative humidity, and the presence or absence of *Verticillium* growth on mite bodies of each stage was recorded.

Sampling eggs in winter and spring

Two cores from which active mites had been collected were selected randomly from each plot (20 cores/week/site), and the vegetation was cut off at ground level. Unhatched eggs on foliage were counted within a day, using a binocular microscope, and host plant recorded (subclover, capeweed, grasses or other plants). Unhatched *H. destructor* eggs are orange in colour and can be readily distinguished from hatched eggs, which are transparent, and from eggs of blue oat mite *Penthaleus major* (Dugès) (Acari: Penthaleidae), which are redder in colour and larger. The efficiency of sampling was checked by searching for further mites and eggs on the soil surface of two cores, selected randomly each week, from which active mites and their eggs had already been sampled.

The viability of eggs laid on pasture in 1992 was tested from both sites. A subsample of 100 eggs was retained weekly from the pasture samples, and placed singly on filter paper over a moist sponge in a Petri dish. The Petri dish was covered with a lid, sealed with Parafilm membrane, put in a constant temperature room at 15°C, and the number of eggs hatching counted weekly. Most eggs hatched in one to two weeks.

Sampling diapause eggs in summer

Diapause eggs were sampled in early December, after the annual pasture plants had senesced and all female mites were dead, but before the cadavers were likely to be blown away during the summer. Ten cores (2–3 cm deep) were collected from the centre line of each block at 3 m intervals (total of 100 samples/site), and placed in plastic bags. The soil was sieved through 0.6 mm aperture mesh to remove the debris, and then through 0.3 mm aperture mesh (0.15 mm diameter wire) which retained the cadavers of the diapausing female mites (Ridsdill-Smith & Annells, 1993). Cadavers of male mites decomposed quickly on the soil surface and were not recovered. Female cadavers were separated from the remaining soil under a dissecting microscope and counted. A sample of 50 of these female cadavers was moistened, dissected, and the number of eggs counted. The mean number of female mite cadavers/core and mean number of diapause eggs/female cadaver was used to calculate the mean number of diapause eggs/core.

Table 1. Mean weekly minimum and maximum temperatures, and weekly rainfall for winter (May–August) and spring (September–October or the end of the period of mite activity), and mean estimates of pasture height and grazing intensity.

Site	Year	Temperature (°C)		Rainfall (mm)			Pasture height (cm)		% times grazing animals present
		May–Aug	Sept–Oct	May–Aug	Sept–Oct	Year	May–Aug	Sept–Oct	
Keysbrook	1990	8.7–18.4	10.0–20.3	421	219	846	7	27	56
	1991	10.4–18.6	11.2–21.2	681	184	1026	4	17	62
	1992	10.3–18.3	9.8–19.5	587	143	978	4	3	81
Narrogin	1991	7.4–16.2	7.8–20.1	344	84	548	3	15	55
	1992	7.6–16.7	6.9–17.5	358	46	608	3	3	71

Rainfall and pasture measurements collected from the sampling sites, and screen temperatures from the nearest meteorology station.

Results

Pastures

Comparisons are made mostly for 1991 and 1992, when data were obtained from both sites. The mean weekly screen temperature in both winter (May–August) and spring (September–October) was lower at Narrogin than Keysbrook, and annual rainfall from May to October at Narrogin in 1991 and 1992 was half that at Keysbrook (table 1). Winter and spring rainfall (May–October) averaged 76% of annual rainfall at both sites. In 1991 and 1992 while mites were active, there were twice as many weeks when 20 mm or less rain fell at Narrogin (19 weeks) than at Keysbrook (9 weeks) (fig. 1). This is taken to indicate that there were more periods when soil would be dry at Narrogin than Keysbrook. Spring temperatures and spring rainfall were lower in 1992 than 1991 at both sites (table 1).

Pasture height in winter (May–August) was slightly lower at Narrogin than at Keysbrook. In spring (September–October), pasture height was four times greater than in winter at both sites, except in 1992 when it did not increase (table 1). The mean dry weight of foliage at Keysbrook during the winter and spring in 1990 averaged 36.6 g/quadrat, equivalent to 2285 kg/ha (unpublished data). Grazing animals were observed on more sampling occasions in 1992 than in 1991 at both sites (table 1).

Subclover covered a greater proportion of the ground than capeweed or grasses (table 2). Subclover and capeweed content decreased in consecutive years while the proportion of the grasses increased (table 2). There were significant changes in pasture composition between 1991 and 1992 at Keysbrook ($\chi^2_2 = 15.39$, $P < 0.01$), and at Narrogin ($\chi^2_2 = 53.32$, $P < 0.001$). The changes in proportions of subclover and of capeweed were similar between years (Keysbrook $\chi^2_2 = 0.74$, NS; Narrogin $\chi^2_1 = 0.00$, NS), while changes in the proportions of subclover plus capeweed and grasses differed between years (Keysbrook $\chi^2_2 = 14.69$, $P < 0.001$; Narrogin $\chi^2_1 = 53.32$, $P < 0.001$).

Active mites in winter and spring

The first peaks of mites in the autumn consisted mainly of eggs, except at Narrogin in 1991 when few eggs were laid (fig. 2). This and further peaks were considered to mark the passing of generations, unless they were four weeks apart or less when they represented the development of cohorts. Generations were easier to see at Keysbrook in 1990 and 1991, when the mite populations were higher. It is concluded from these data that *H. destructor* probably completed three generations during the year. Synchronization of generations became less pronounced during the season. The average composition of populations over all sites and years at the first peak was 65% eggs, 21% young mites (larvae, protonymphs and deutonymphs) and 14% old mites (tritonymphs and adults). The second generation peak consisted of 49% eggs, 33% young mites and 18% old mites. These age distributions

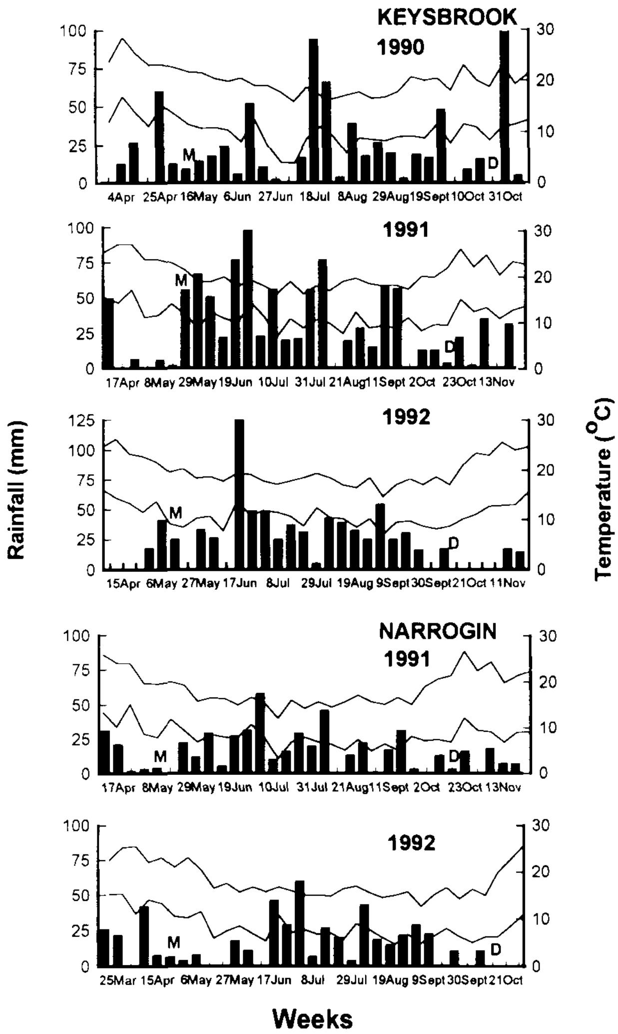

Fig. 1. Weekly rainfall at Keysbrook and Narrogin sampling sites, and mean weekly maximum and minimum temperatures at nearby meteorology stations. Week in which *Halotydeus destructor* first appeared (M) and week in which over 90% of mature adult mites contained diapause eggs (D).

Table 2. Mean (±SE) proportion of ground covered by the main pasture species groups at each site, and the proportion of mite eggs laid on each pasture species group.

Site	Year	Subclover (%)		Capeweed (%)		Grasses (%)	
		Pasture	Eggs	Pasture	Eggs	Pasture	Eggs
Keysbrook	1990	57 ± 6	62 ± 2	27 ± 6	32 ± 2	12 ± 1	5 ± 1
	1991	45 ± 7	61 ± 6	20 ± 3	32 ± 5	25 ± 2	7 ± 2
	1992	41 ± 6	74 ± 5	14 ± 1	21 ± 4	32 ± 4	2 ± 1
Narrogin	1991	55 ± 6	74 ± 5	22 ± 4	23 ± 5	21 ± 3	1 ± 1
	1992	17 ± 4	91 ± 2	7 ± 1	4 ± 1	69 ± 5	1 ± 1
Mean		43	72	18	22	32	3

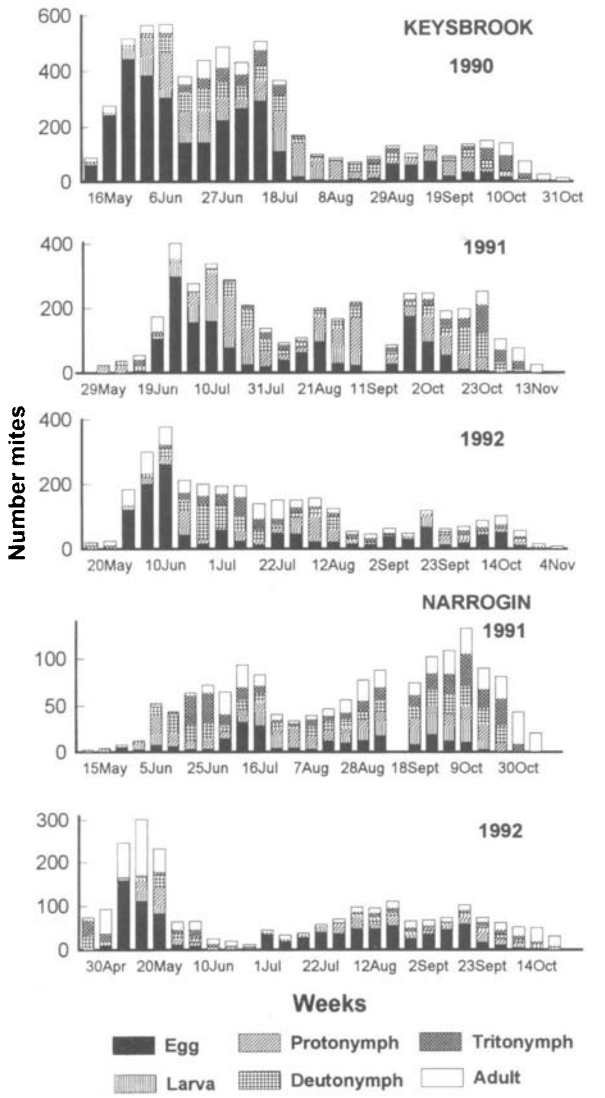

Fig. 2. Mean weekly number of *Halotydeus destructor* eggs, larvae, protonymphs, deutonymphs, tritonymphs and adults/core in grazed pastures at Keysbrook and Narrogin sampling sites.

are consistent with increasing populations. The third generation peak consisted of 24% eggs, 38% young mites and 38% old mites. This is consistent with a falling population, but included adult mature females which were retaining eggs rather than laying them (see below). At Narrogin in 1992, the first peak contained mostly old mites (37% eggs, 18% young mites and 45% old mites), but subsequent peaks contained mostly eggs.

Peaks of active mites (i.e. excluding eggs) indicated the passing of generations, and numbers over the peaks represented weeks to each generation since mites first emerged (fig. 3). The first peak at each site occurred on average seven weeks after the first active mites were detected in the pasture, and there was an average of eight weeks between subsequent peaks at all sites (fig. 3). The mean weekly mite numbers for each year and site were not significantly correlated with rainfall (mean $r^2 = 0.038$), or maximum (mean $r^2 = 0.050$) or minimum (mean $r^2 = 0.028$) temperatures for the previous week (range for all correlations $r^2 = 0.0003$–0.171).

Active individuals of *H. destructor* were present mostly from May to October, an average period of 27 weeks (table 3). In 1991 and 1992, when data were available from both sites, there were significantly more active mites at Keysbrook (89 mites/core equivalent to 11,300 mites/m^2) than at Narrogin (50 mites/core equivalent to 6400 mites/m^2) (table 3). The peak numbers were 1.9 times the mean *H. destructor* populations, and were assumed to represent a density at which shortage of some resource caused population regulation. *Halotydeus destructor* numbers appeared not to increase in the spring of 1992 at both sites (fig. 3).

The corer worked well in all weather conditions. Efficiency of sampling for active mites was very high. Altogether 246 cores were checked, which contained 603 *H.*

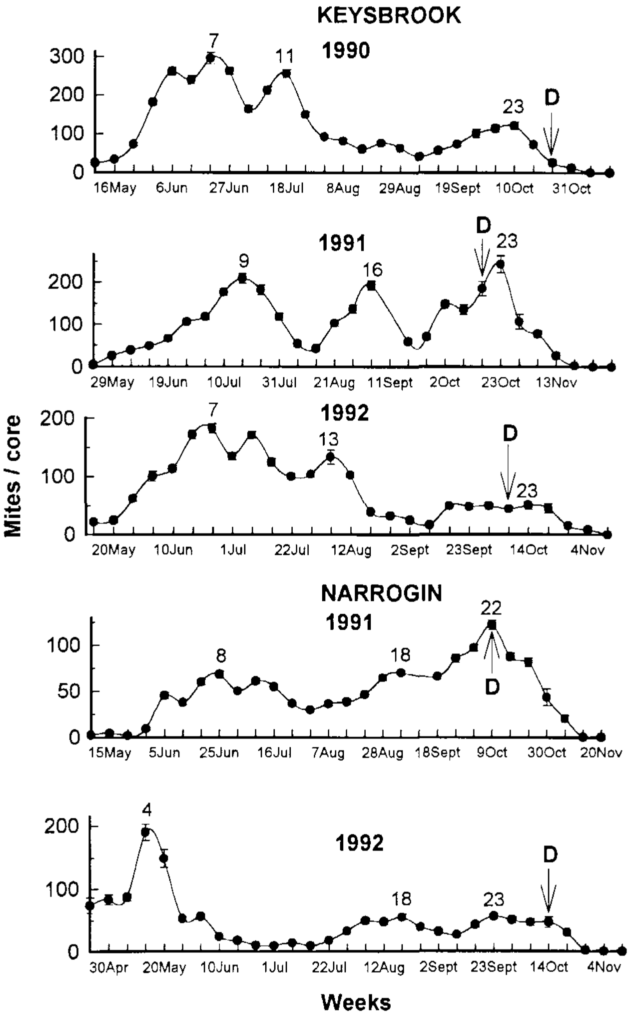

Fig. 3. Mean number of active *Halotydeus destructor*/core (±SE) in grazed pastures at Keysbrook and Narrogin sampling sites. Numbers are weeks from the emergence of mites to peaks of abundance representing generations. D is the week in which over 90% of mature adult female mites contained diapause eggs.

Table 3. Means (±SE) of active *Halotydeus destructor*/core and of eggs laid/core, and period of mite activity and of egg laying.

Site	Year	Period of mite activity		Mean/core[a]		Period of egg laying
		Dates	Weeks	Active mites	Eggs	Dates
Keysbrook	1990	10 May–31 Oct	26	121 ± 17 (224)	125 ± 27 (271)	10 May–17 Oct
	1991	22 May–20 Nov	27	103 ± 13 (215)	79 ± 17 (190)	12 June–23 Oct
	1992	13 May–4 Nov	26	76 ± 10 (122)	55 ± 14 (128)	27 May–21 Oct
Narrogin	1991	8 May–6 Nov	27	51 ± 6 (87)	11 ± 2 (23)	22 May–16 Oct
	1992	22 Apr–28 Oct	28	49 ± 8 (100)	35 ± 7 (92)	20 Apr–21 Oct
F ratios for 1991–1992						
Site				16.06***	18.63***	
Year				2.14	0	
Site × year				1.67	5.89*	

[a]Figures in brackets are average peak numbers for each generation.
Analyses of variance to compare sites for 1991 and 1992, *$P < 0.05$, ***$P < 0.001$.

destructor, compared with 17,743 collected from these cores during normal sampling (97% recovery). Efficiency of sampling for eggs was also high, with 102 eggs collected from check cores, compared with 8654 previously collected from the cores (99% recovery).

Disease

The proportion of active mites showing symptoms of the fungal disease, *N. acaridis*, was very low. There was an average of 3.7% and 1.3% diseased at Keysbrook, and 0% and 0.7% at Narrogin, in 1991 and 1992 respectively. The disease symptoms were observed mainly in older mites, with 62% of diseased mites being adults, 28% tritonymphs and 10% deutonymphs. At Keysbrook between 9 October and 6 November 1991, a maximum of just over 20% of adult mites showed symptoms of *N. acaridis*; the highest levels observed. In 1992 at Narrogin, between 21 October and 11 November, 15% of adult female mites which were dissected had disease symptoms; they contained large white lumps, or the eggs were clear. Diseased adult female mites contained 19.8 ± 0.6 diapausing eggs each (n = 120), which was significantly less than healthy adult female mites that contained 38.6 ± 0.6 diapausing eggs each (n = 211) (a 49% reduction) (t_{329} = 19.44, $P < 0.001$). The disease may therefore be affecting numbers of diapause eggs produced by *H. destructor* in spring.

None of the mites field-collected from Toodyay showed evidence of *Verticillium* with either washing treatment, while the fungus *Aspergillus*, penicillin and bacteria grew on the plates.

Egg-laying in winter and spring

Three peaks of egg-laying could usually be distinguished through the season, starting on average five weeks after the first mite emerged, and seven weeks apart (fig. 4). Weeks to each peak since mites emerged are given over the peaks. Peaks of egg laying were generally two to three weeks before the peaks of active mites. The average number of eggs laid in 1991 and 1992 was three times greater at Keysbrook than Narrogin (table 3). Peak egg populations were 2.4 times greater than the mean *Halotydeus destructor* egg populations. There were no differences between the numbers of eggs laid in 1991 and 1992 at Keysbrook, with a mean of 67 eggs/core, equivalent to 8500/m². At Narrogin fewer eggs were laid in 1991, when there were 11 eggs/core equivalent to 1400/m², than in 1992, when there were 35 eggs/core, equivalent to 4500/m² (table 3).

The proportion of adult mites which were female

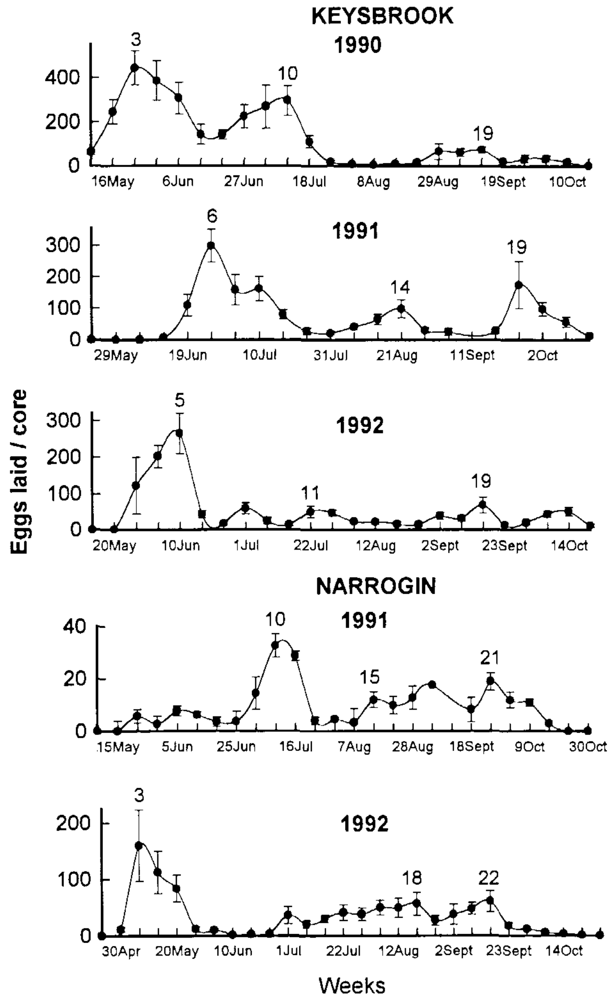

Fig. 4. Mean weekly number of *Halotydeus destructor* eggs/core (±SE) in grazed pastures through the period of activity at Keysbrook and Narrogin sampling sites. Numbers represent weeks from the emergence of mites to peaks of egg abundance representing generations.

Table 4. Factors affecting numbers of eggs laid. Means (±SE) from weekly samples of the proportion of adult female mites, numbers of developed eggs dissected from mature adult female mites in winter and spring, and numbers of eggs laid for every adult female present in that week.

Site	Year	Proportion females	Dissected eggs/female		Eggs laid/adult female
			May–Aug	Sept–Nov	
Keysbrook	1990	0.748 ± 0.027	9.5 ± 0.9	28.1 ± 3.0	9.9 ± 1.7
	1991	0.682 ± 0.024	8.8 ± 0.9	19.1 ± 2.8	11.7 ± 2.5
	1992	0.657 ± 0.021	7.7 ± 1.1	22.7 ± 3.5	10.1 ± 1.7
Narrogin	1991	0.850 ± 0.039	8.4 ± 1.0	15.3 ± 2.0	4.2 ± 1.5
	1992	0.775 ± 0.012	9.7 ± 0.7	19.0 ± 3.5	8.8 ± 1.8
F ratios for 1991–1992					
Site		31.49***	0.27	1.71	6.17*
Year		3.88	0.31	1.67	0.77
Site × year		0.96	1.03	0.001	3.06

Analyses of variance to compare sites for 1991 and 1992, $^{*}P<0.05$, $^{***}P<0.001$.

throughout the season, was significantly greater than 0.5 at both sites in all years (χ^2_1 for numbers against a 1:1 ratio ranged from 178.9 to 4758.6, $P<0.001$). The proportion of adults which were female was significantly lower at Keysbrook (0.669) than at Narrogin (0.813), but there was no difference between 1991 and 1992 (table 4). Fewer eggs were laid/adult female present at Narrogin (6.5), where the proportion of female mites was greater, than at Keysbrook (10.9) (table 4).

Immature adult female mites were expected to contain few developed eggs, and there was an average of 1.9 developed eggs/mite in 1992 at both sites. However, mature adult female mites, during the winter (May till August) in 1991 and 1992, contained an average of 8.8 developed eggs with no differences between sites and years (table 4). In the spring (September till November), there were 20.8 eggs/mature female (maximum of 100 eggs in a single female) with no differences between sites and years (table 4). Eggs collected from vegetation in 1992 hatched readily in the laboratory throughout the season with 91% hatch from Keysbrook and 93% from Narrogin. There was one week at each site on 29 July when the mean hatch rate was 37%, and no explanation can be given for this.

Looking at the spring data separately, there were nearly three times fewer mites, and three times fewer adult female mites in 1992 than 1991 at both sites, but no difference in the number of eggs laid between years (table 5). Between sites there was no difference in the number of mites, but there were 31% fewer adult female mites at Keysbrook than Narrogin, and three times more eggs laid at Keysbrook than at Narrogin (table 5).

Most eggs (72%) were laid by *H. destructor* on subclover, and least on grasses (table 2). The proportion of eggs laid on subclover did not vary from the proportion of subclover in the ground cover at Keysbrook in 1990 ($\chi^2_1=0.22$, NS) or 1991 ($\chi^2_1=2.32$, NS). A greater proportion of eggs were laid on subclover relative to the proportion of subclover in the pasture at Keysbrook in 1992 ($\chi^2_1=16.64$, $P>0.001$), and at Narrogin in 1991 ($\chi^2_1=8.19$, $P>0.01$) and 1992 ($\chi^2_1=112.92$, $P>0.001$) (table 2). There was no correlation between the mean annual subclover content and mean number of eggs laid for 1991 and 1992 at the two sites ($r^2=0.005$, 3df, NS).

Timing of mite emergence and production of diapause eggs

The emergence of active *H. destructor* in autumn did not seem to follow any particular weekly pattern of rainfall (fig. 1). When the mean weekly maximum temperature for six weeks before and after mite emergence was plotted, the first appearance of active mites was predicted by the week in which the mean weekly maximum temperature fell below 21.5°C ($r^2=0.876$, 70df, $P<0.001$) (fig. 5). It is not known to what extent all mites hatched in the same week.

In spring, the proportion of diapause eggs dissected from adult female mites increased very rapidly between 3 and 24 October (fig. 6). The last winter eggs were laid between 16 and 23 October (table 3). At Narrogin, the date on which

Table 5. Spring data for *Halotydeus destructor* abundance. Mean (±SE) number of mites, number of adult female mites and number of eggs laid.

Site	Year	Mites/core	Adult female mites/core	Eggs laid/core
Keysbrook	1990	68.7 ± 12.8	13.4 ± 3.8	35.1 ± 9.5
	1991	113.2 ± 22.6	15.7 ± 3.1	57.5 ± 22.8
	1992	35.1 ± 5.3	3.9 ± 0.5	35.1 ± 7.0
Narrogin	1991	74.7 ± 9.9	21.6 ± 2.1	11.7 ± 2.4
	1992	37.0 ± 5.5	6.7 ± 1.1	23.1 ± 7.9
F ratios for 1991–1992				
Site		1.49	4.74*	5.89*
Year		20.04***	44.88***	0.21
Site × year		1.85	0.66	2.10

Analyses of variance to compare sites for 1991 and 1992, $^{*}P<0.05$, $^{***}P<0.001$.

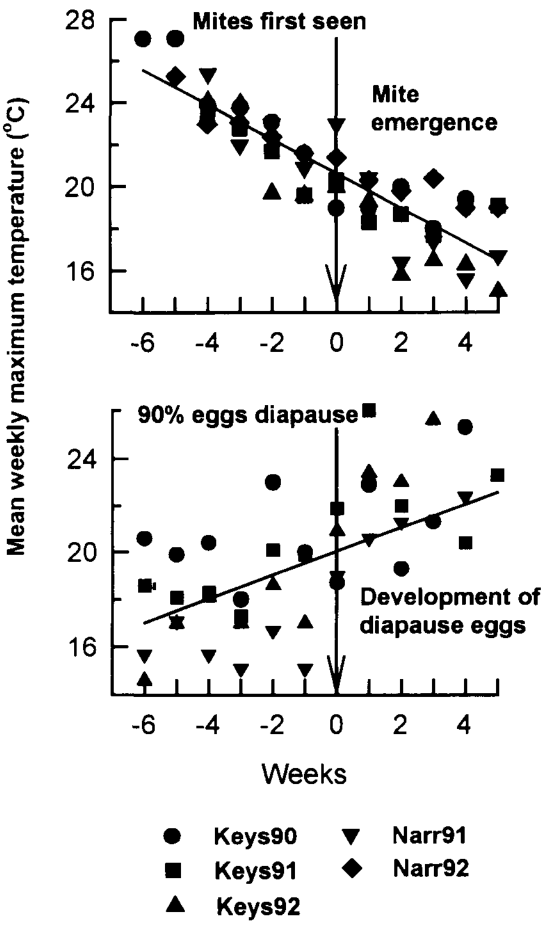

Fig. 5. Mean weekly maximum temperatures for six weeks before and five weeks after *Halotydeus destructor* emergence, and six weeks before and five weeks after the appearance of 90% diapause eggs. Linear regressions fitted to data from sites (Keys, Narr) and years (90, 91, 92).

dissected adult female mites contained 90% of diapause eggs was estimated for 1992 (figs 1 and 3), but other data were missing and the plot over time could not be confidently drawn. When the mean weekly maximum temperatures were plotted for six weeks before and five after the

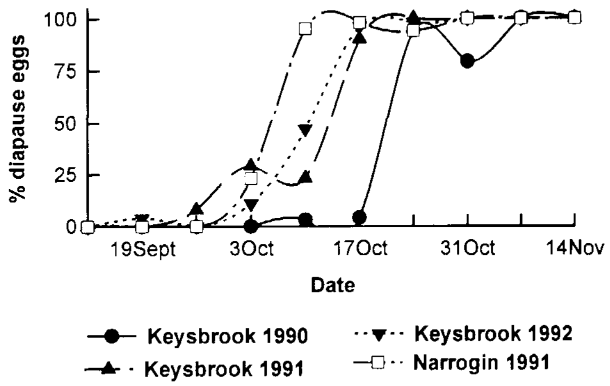

Fig. 6. Spring appearance of diapause eggs in dissected mature adult female *Halotydeus destructor* in different years and sites.

occurrence of the week in which 90% diapause eggs occurred, diapause was predicted when the temperature increased above 20°C ($r^2 = 0.448$, 43df, $P < 0.01$) (fig. 5). Mites were often abundant in pasture for several weeks following the development of diapause eggs (fig. 3). Numbers of active mites could not therefore be used to predict the presence of diapause eggs.

Oversummering diapause eggs

There were five times more female cadavers in 1991 than in 1992 at both sites, and in 1991 there were 37% more female cadavers at Narrogin than at Keysbrook (site × year interaction) (table 6). There were 60% more diapause eggs/female cadaver in 1992 than 1991 at Keysbrook, but not at Narrogin (site × year interaction). On average there were four times more diapause eggs (number female cadavers × number of diapause eggs/cadaver) at both sites in 1991 (1162 diapause eggs/core) than in 1992 (287 diapause eggs/core) (table 6). These were equivalent to 148,000 and 36,600 diapause eggs/m² respectively.

Discussion

Average abundance of active *H. destructor* at the Keysbrook site was nearly twice that at the Narrogin site, whereas the period of activity (27 weeks) from May–October was the same at both sites. Three times more eggs were laid

Table 6. Mean numbers (±SE) of female cadavers and diapause eggs present in the soil in December.

Site	Year	Mean number (±SE)		
		Female cadavers/core	Diapause eggs/female cadaver	Diapause eggs/core
Keysbrook	1990	20 ± 3	38 ± 1	760
	1991	30 ± 3	30 ± 1	930
	1992	9 ± 2	48 ± 1	414
Narrogin	1991	41 ± 5	35 ± 1	1394
	1992	5 ± 1	33 ± 1	160
F ratios for 1991–1992				
Site		1.08	37.41***	
Year		85.12***	157.24***	
Site × year		5.86*	184.08***	

Analyses of variance to compare sites for 1991 and 1992, *$P < 0.05$, ***$P < 0.001$.
Diapause eggs = (number cadavers × number eggs/cadaver).

at Keysbrook than at Narrogin, and the egg numbers fluctuated more during the season than the mite numbers. These fluctuations are consistent with population size being regulated, probably through numbers of eggs laid. The use of the corer for sampling was efficient and unbiased over different conditions, recovering 97% of active mites and 99% of eggs present in the pasture.

Immature adults feed to develop their eggs. Since the mean number of fully developed eggs dissected from mature adult female *H. destructor* were similar at both sites and more eggs were laid at Keysbrook, it was the rate of oviposition that varied. Low numbers of *H. destructor* eggs were laid at Narrogin throughout 1991, but no explanation can be given for this here. Nutritional quality of the plant species strongly influences *H. destructor* rate of multiplication (Annells & Ridsdill-Smith, 1994), and could be affecting mite abundance at the pasture sites. The fecundity of the two-spotted spider mite is positively related to the nitrogen content of the leaves they feed on (Wermelinger *et al.*, 1991; Wilson, 1994). *Halotydeus destructor* prefer and select subclover for feeding (Gaull & Ridsdill-Smith, 1996) and for oviposition (this paper). However, the subclover content of a pasture did not determine the number of *H. destructor* eggs laid. Instead, it is suggested that better food quality and plant growth caused the mites to lay more eggs at Keysbrook. The population growth of another plant-feeding mite species, the cassava green mite, *Mononychellus tanajoa* (Bondar) (Acari: Tetranychidae), is limited in part by food depletion caused by the mite (Skovgard *et al.*, 1993).

Although there was a mix of stages present at any one time, it is suggested that *H. destructor* completed three generations a year. Each *H. destructor* generation in pastures took seven to eight weeks, using the peak numbers of mites plus eggs, or active mites, or eggs, as markers. In the laboratory at 11–18°C (temperature range similar to that at the pasture sites), *H. destructor* completed a generation every five weeks continuously, with no evidence of diapause (Ridsdill-Smith & Gaull, 1995). The slower rate of development in pastures may be related to a general lower availability of food of suitable quality, and to less favourable environmental effects.

Pasture growth was probably greater at Keysbrook than Narrogin. Rainfall at Keysbrook during the period of mite activity was about twice that at Narrogin, and temperatures were about 2°C greater. Dry matter production in annual legume-based pasture systems in southwestern Australia is predicted to increase with rainfall up to 440 mm, while at higher rainfall water-logging can limit growth (Bolger *et al.*, 1993). There was less than 20 mm rain in 33% of the weeks that mites were active at Keysbrook and in 70% of the weeks at Narrogin. Dry periods, which might restrict pasture growth and cause mite mortality, were more frequent at Narrogin.

Sex ratio can influence the reproductive capacity of a population and thus population size. Although there were more adult female than male *H. destructor* at both sites, the sex ratio (proportion of females) was lower at Keysbrook than at Narrogin. The proportion of females was 21% greater at Narrogin, and there were 40% fewer eggs laid/adult female. This is consistent with the model of Trivers & Willard (1973) that female-biased sex ratios are more likely as female condition declines. Plant-feeding spider mites show female-biased sex ratios, and the proportion of females is greater when parents feed on poorer quality leaves (Wrensch & Young, 1978). Possibly the sex ratio became more female biased in response to lower food availability at Narrogin, or to greater mortality of males.

No biotic factor was observed to be having a major impact on the abundance of active *H. destructor*, as was also found by Swan (1934) and Norris (1938). Symptoms of a pathogenic fungus, *N. acaridis*, were evident in less than 4% of mites in pastures. The fungus was more common in adult *H. destructor* and most diseased adults were seen at Keysbrook, where rainfall was greater. *Neozygites* sp. epizootics can build up rapidly in two-spotted spider mite populations when humidity is high (Brandenburg & Kennedy, 1982; Klubertanz *et al.*, 1991). Another fungus, *Verticillium* sp., which caused *H. destructor* mortality in the laboratory (Ridsdill-Smith & Gaull, 1995), was not found attacking mites in pastures. Predatory mites were seen infrequently at these sites and were not counted.

Numbers of active mites were lower in spring of 1992 than 1991, but numbers of eggs laid were not. Rates of hatch in the laboratory for eggs collected from vegetation were high at both sites, as was also found by Wallace (1970b). In spring 1992, rainfall was less, temperatures were lower, grazing was more intense and pasture was shorter, than in 1991 at both sites. Grimm *et al.* (1994) found that *H. destructor* abundance was significantly reduced when the quantity of pasture available was reduced by increased grazing intensity of sheep. We suggest that active mite mortality was higher in spring of 1992 than 1991 in our study, and in the grazing study of Grimm *et al.* (1994), due to lower relative humidity at the soil surface. In small scale laboratory studies, the survival period of *H. destructor* is greater the higher the relative humidity; with an optimum near saturation (Solomon, 1937).

Factors that reduced numbers of *H. destructor* in spring also reduced numbers of diapausing eggs in summer. In 1992, there were three times fewer mites in spring, and four times fewer diapause eggs in summer, than in 1991 (148,000 and 36,600/m^2). Spraying *H. destructor* during spring in a small-scale trial resulted in a 94% reduction in numbers of oversummering eggs (Ridsdill-Smith & Annells, 1993). We believe that biological or chemical control of *H. destructor* in pastures in spring will have the potential to achieve benefits both in the spring and the following autumn, whereas spraying in autumn will provide benefits only in autumn.

However, correct timing is important for effective control with chemicals. In autumn, *H. destructor* should be sprayed within 2–3 weeks of emergence, before damage is severe. We predict that active *H. destructor* will appear in autumn when the mean weekly maximum temperature falls below 21.5°C, as shown by the data of Wallace (1970b). In spring, *H. destructor* should be controlled just before diapause eggs are produced, which is predicted to occur when the mean weekly maximum temperature increases to 20°C, but the correlation is not as good as that for autumn emergence. Two sprays of a systemic insecticide in early September could give a 98% reduction in *H. destructor* numbers the following autumn, but if the spraying is delayed until November the reduction is only 58% (Seidel, 1995). Wallace (1970a) suggests that initiation of diapause is stimulated by the maturation of pasture plants in spring, and especially capeweed. However, *H. destructor* produces diapause eggs at the same time in pasture in the presence or absence of capeweed (R. Chapman, unpublished data), and we suggest that other factors are involved.

In summary, we suggest that two factors are chiefly responsible for regulating *H. destructor* abundance. These are the rate of oviposition, which appears to be the main cause of differences in abundance between Keysbrook and Narrogin, and the mortality of active mites, which appears to be the main cause of differences in abundance between spring in 1991 and 1992 at both sites. These are the characteristics of an opportunist species.

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