ECOLOGY AND BEHAVIOR

Competitive Interactions Between Two Pest Species of Earth Mites, Halotydeus destructor and Penthaeleus major (Acarina: Penthaleidae)

A. R. Weeks and A. A. Hoffmann

Centre for Environmental Stress and Adaptation Research, La Trobe University, Bundoora, Victoria, 3083, Australia


ABSTRACT Competition was investigated between two pest earth mite species, Penthaeleus major Dugés and Halotydeus destructor Tucker, which occur sympatrically and are major pests of southern Australian pastures and crops. Three geographically separate pasture sites within Victoria were sampled monthly. Abundance patterns were similar across sites in that there was a marked increase in numbers of H. destructor in spring. Field competition plots were set up on pasture. In the first season, H. destructor had a negative effect on P. major but not vice versa. During the summer, diapause and ensuing generation, density-dependent (intraspecific) competition was evident in P. major but not in H. destructor. The interspecific asymmetry was switched in the following season, with P. major dominating most plots and having a negative effect on the reproductive output of H. destructor. These findings indicate that suppression or eradication of one species of earth mite from pastures may result in another species increasing in relative abundance.

KEY WORDS Penthaeleus, Halotydeus, earth mite, competition, displacement

Earth mite species are agricultural pests in southern Australia and other parts of the world in both pastures and crops. There are two main types of earth mites: Halotydeus destructor (Tucker) (Acari: Penthaleidae), and the blue oat mite complex Penthaeleus spp. The latter consists of at least three species, P. major (Dugés) (Acari: Penthaleidae), P. falcatus (Qin & Halliday), and an undescribed species (Weeks and Hoffmann 1999). Earth mites are usually controlled by chemicals although programs have been established to develop plants resistant to H. destructor (Jiang and Tucker, which occur sympatrically and are major pests of southern Australia, although P. major extends into drier inland regions (Wallace and Mahon 1971) and higher rainfall areas. The mites are active in the field during winter from April to late October with two or three generations occurring each season. In spring the mites produce diapause eggs to survive the unfavorable summer conditions. The larvae hatch the following autumn. H. destructor reproduces sexually (Annells 1994, Weeks et al. 1995), whereas P. major is an obligate parthenogen and populations are made up of clones (Weeks et al. 1995, Weeks and Hoffmann 1998).

Herein, three questions are addressed relating to the competitive interactions of P. major and H. destructor in the field. First, what are the seasonal abundance patterns of P. major and H. destructor in the field? Three geographically distinct sites were sampled monthly during 1995 to address this question. Second, does interspecific competition occur between P. major and H. destructor? This was tested by setting up field plots in a pasture and by releasing P. major, H.
By taking advantage of different frequencies of *P. major* and *H. destructor* present in the field plots at the end of the first season, we could test whether the growth rate of one species depended on the frequency of the other species. Finally, is there evidence of intraspecific as well as interspecific competition? This was tested by examining the impact of the density of conspecifics on growth rate with regression techniques (Varley et al. 1975, Begon et al. 1996).

**Materials and Methods**

**Seasonal Abundance.** The seasonal patterns of *P. major* and *H. destructor* were investigated in pasture at three different sites in Victoria during 1995. Monthly samples were taken from Derrimut (144° 45' W, 37° 52' N), Ballarat (143° 52' W, 37° 33' N), and Yanakie (146° 15' W, 38° 50' N) from April to November. At each site, an area (15 by 10 m) was pegged out and 10 samples were randomly taken from this area each month. For each sample, a 15-cm² metal frame was pushed into the ground. All mites and other arthropods within the frame were carefully collected with a vacuum pooter and placed into a vial. The vial was then filled with 70% ethanol to preserve earth mites and other arthropods for subsequent identification. The major plant types found at Derrimut and Yanakie were capeweed (*Arctocephalus calendula* L.), clover (*Trifolium* ssp.), and various grass species (*Poa* ssp.), whereas at Ballarat there were grasses, clover, and cat’s ear (*Hypochoeris* spp.).

**Field Plots.** At the start of 1996 an experiment was set up in pasture at Broadford (145° 4' W, 37° 11' N) to investigate the competitive interactions in *P. major* and *H. destructor* in the field. An area (16 by 35 m) was fenced off from the rest of the pasture to stop livestock entering the site. Twenty-eight plots (2 by 2 m) were set up within this fenced area on 16 April 1996, before hatching of *P. major* and *H. destructor* diapause eggs. White plastic sheets (95 cm high, 0.5 cm thick) as described in Weeks and Hoffmann (1998) were erected as barriers around the plots. To prevent mite movement, the sheets were inserted 15 cm into the ground, and Tac Gel (Rentokil, Chatswood, NSW, active ingredient polybutene) was applied to their outer upper edges to trap any mites climbing up the sheets. The plots mostly contained three plant types, Yorkshire fog grass (*Holcus lanatus* L.), clover (*Trifolium* ssp.), and phalaris (*Phalaris* ssp.). Once mites had hatched from diapause (4 May), all resident earth mites within the plots were eliminated by spraying three times (10 d apart) with the organophosphate Imidan (Cropcare, Strathpine, Australia, applied at the rate 350 ml/ha). The plots were then left for an additional 10 d after the last spray before introducing the mites (the residual effect of Imidan is ~6 d).

Three different treatments replicated eight times were assigned randomly to the plots, and four plots acted as controls (no mites added). The three treatments were as follows: (1) 3,200 *P. major* (800 mites per square meter), (2) 3,200 *H. destructor*, and (3) 3,200 *P. major* + 3,200 *H. destructor* (1,600 mites per square meter). This simple design allows the assessment of interspecific competition without confounding effects (Underwood 1986). Both *P. major* and *H. destructor* were collected from the surrounding pasture at Broadford and brought back to the laboratory. Over a 5-d period, mites were sorted and counted and transferred to the plots. Only adult mites were introduced and these were stored at 11°C before release to prevent mite mortality. Tac Gel was reapplied to the outer upper edges of the barriers when needed.

Plots were sampled for mite abundance at the end of the season (1 November), when almost all *P. major* and *H. destructor* were at the adult stage and producing diapause eggs. Sampling involved removing a core of 10.5 cm in diameter with a metal frame (Wallace 1956, Ridsdill-Smith and Annells 1997). The corer was driven 5—10 cm into the ground, inverted over a funnel, and tapped with a rubber mallet to release mites into a vial. Vials were labeled and the vial was then filled with 70% ethanol. Six samples were taken randomly per plot. Species were identified and counted under a dissecting microscope.

Plots were sampled again at the start of the next season (28 May 1997), after diapause had been broken and almost all mites were at the adult stage. Six samples were again taken randomly per plot. The barrier of one of the plots where *H. destructor* had been introduced came away from the soil surface during the summer months and this plot was therefore not sampled.

In the plots where only one of the species had been introduced, very low numbers of the other species were present by the end of 1996 (see below). This was probably caused by the release of the incorrect species as well as by mites occasionally passing the barriers. A low level of movement across the barriers also is suggested by a few earth mites found in two of the control plots (see below).

Because of mite movement and competitive effects, a range of *P. major* and *H. destructor* numbers existed across plots at the start of the 1997 season. All 23 plots were therefore treated as independent data points and used to test for frequency-dependent competition as well as comparing the intensity of interspecific with intraspecific competition. Plots were sampled at the end of the season (15 September) by taking six random samples per plot. We collected this final sample earlier than in 1996 because of abnormally dry conditions. Earth mites hatched diapause eggs much earlier than usual as a consequence of these conditions.

During the course of the field experiment, the seasonal abundance patterns of *P. major* and *H. destructor* were determined in pasture adjacent to the plots within the fenced area. An area (15 by 5 m) was pegged out and 10 random samples were taken six times between July and November in 1996 and five times between May and September in 1997. The core sampling method was used as described above.

**Data Analysis.** To analyze the field competition data, samples were converted to numbers of mites per square meter. During the first season, $R_0$ (Stearns
1992) was calculated for each species in each plot as the number of adult mites collected at the end of the season divided by the number placed into the plot at the start of the season. \( R_0 \) also was calculated for each plot through diapause (number of adults at start of second season divided by number at end of first season) and for the second season (number at end divided by that at beginning of second season). To achieve normality and facilitate interpretation, all \( R_0 \) values were log10 transformed for analyses. Note that reproductive output (after log10 transformation) is equal to \((-1)k\), where \( k \) is the killing value often used by population ecologists (Varley et al. 1975).

To determine if interspecific competition occurred in the first season, the mean \( R_0 \) values for the pure treatments were compared with the mixed treatments for \( P. major \) and \( H. destructor \) with \( t \)-tests. The same procedure was used to compare \( R_0 \) values for pure and mixed treatments through diapause. Multiple regression was used to determine if \( R_0 \) through the diapause generation was dependent on \( N_b \), the number of \( H. destructor \) and \( P. major \) at the end of the previous season. Both pure and mixed plots for a species were considered, and \( N_b \) values were log10 transformed before analysis. Multiple regression allowed the relative strength of interspecific competition and intraspecific competition to be compared by examining the partial regression coefficients.

Multiple regression also was used to analyze plot data from the second season to determine the presence of inter- or intraspecific competition (frequency or density dependence). Again, \( R_0 \) values for the plots were regressed on \( N_b \).

Results

Seasonal Abundance Patterns. The patterns of \( P. major \) and \( H. destructor \) at Derrimut, Ballarat, and Yanakie are shown in Fig. 1. The same overall pattern was found across the sites, although peak numbers differed at each site by up to 10-fold. The abundance of \( P. major \) stayed relatively stable at each of the sites throughout the season. This is in contrast to \( H. destructor \), which increased up to 10-fold in autumn just before diapause. This autumn peak was found at all three sites, although the Yanakie site also had a small peak at the start of winter. At Derrimut and Yanakie, the abundance of \( P. major \) at the start of the season was similar to \( H. destructor \), whereas at Ballarat \( P. major \) was relatively more abundant. No correlations were found between the abundance of predatory mites and other arthropods and the abundance of \( P. major \) or \( H. destructor \) for any of the collections (data not shown).

\( H. destructor \) numbers peaked earlier at Derrimut compared with the other sites, probably reflecting the drier conditions at this site.

Field Plots. Mean mite numbers increased in all three treatments during the 1996 field season from their initial starting numbers (Table 1). Barriers around the plots were largely successful in excluding...
mites; control plots contained a mean of <80 mites per square meter for each species by the end of 1996. There was some contamination from the excluded species in the plots established with one species, but this only averaged ~50 mites per square meter.

Comparisons between pure and mixed plots for reproductive output (Fig. 2) showed that asymmetrical interspecific competition occurred during the 1996 field season. In the pure plots, the reproductive output of *P. major* was significantly higher than in the mixed plots (*t* = 4.98, df = 7, *P* < 0.001), indicating that *H. destructor* had a negative impact on the reproductive output of *P. major*. In contrast, no difference was found between pure and mixed plots for *H. destructor* (*t* = 0.05, df = 7, *P* > 0.05), indicating that *P. major* did not affect the reproductive output of *H. destructor*.

At the start of the 1997 season, there was an increase in mite densities compared with the end of the previous season in all plots (Table 1). In particular, there was a marked increase in *P. major* in the "pure" *H. destructor* treatment and in *H. destructor* numbers in the "pure" *P. major* treatment. There were differences in reproductive output between the pure and mixed treatments over this period (Fig. 2). The mixed plots had a significantly greater *R₀* for *P. major* than the pure plots (*t* = 2.91, df = 7, *P* < 0.05). When data from the pure and mixed plots are considered as independent points, linear regression indicated a significant negative relationship (slope = −0.517 ± 0.152, *F* = 11.60; df = 1, 15; *P* < 0.01) between *R₀* and *Nₐ*, the number of *P. major* at the preceding sampling date (Fig. 3). Plots with higher densities of *P. major* therefore had lower reproductive outputs over the diapause generation. This may reflect intraspecific competition at the juvenile stage, which feeds on nonplant material (Maclean et al. 1998).

It is unlikely that interspecific interactions had much effect on *P. major* numbers over the diapause generation because *H. destructor* numbers were relatively high in mixed plots where *P. major* had a high reproductive output. To test this further, multiple regression was undertaken to control for the number of

![Graph](image)

**Fig. 2.** Mean reproductive output (*R₀*) of *P. major* (BOM) and *H. destructor* (RLEM) in pure and mixed plots at Broadford during the 1996 season and through diapause (end of 1996 through to adult stage at the start of 1997 season).
H. destructor at the preceding sampling date. The partial regression coefficient for $R_0$ regressed against $N_b$ (for P. major) was significant ($b = -0.739 \pm 0.212, t = 3.478, P < 0.01$), whereas the coefficient for $R_0$ regressed against $N_b$ (for H. destructor) was not ($b = -0.079 \pm 0.055, t = 1.44$). Therefore, only intraspecific competition (density dependence) was responsible for the association between $R_0$ and P. major numbers.

Some information about the nature of the competitive interaction within species can be obtained from the partial regression coefficient for $R_0$ regressed against $N_b$ (for P. major). When this coefficient does not differ significantly from a slope of $-1$ (or $+1$ for $k$), it suggests contest rather than scramble competition (Nicholson 1954, Varley et al. 1975, Begon et al. 1996). In scramble competition, all individuals get an equal share of resources but less than needed and they have suppressed reproduction or even die. In contest competition, a number of individuals still get an equal and adequate share of resources, whereas others do not. Under this type of competition, the regression coefficient should not differ from $-1$, whereas under scramble competition it should be less than $-1$ (or $>1$ for $k$). In this current study, the regression coefficient was not significantly different from a slope of $-1$ ($t = 1.23, P > 0.05$), suggesting contest competition.

No differences were found between the reproductive output of H. destructor in the pure and mixed treatments ($t = 0.51, df = 13, P > 0.05$). Moreover, there was no association between the $R_0$ of H. destructor and number of H. destructor at the end of 1996 ($b = -0.123 \pm 0.211, t = 0.584, P > 0.05$) after controlling for the number of P. major at the end of 1996 with multiple regression. Thus, there is no evidence for competition affecting the diapause generation of H. destructor.

The 23 plots remaining at the start of the 1997 field season provided a range of frequencies of P. major and H. destructor. These plots were sampled at the end of the 1997 season to test for density- and frequency-dependent effects. Linear regression indicated a significant negative relationship ($b = -1.32 \pm 0.114, t = 11.39, P < 0.001$) between $R_0$ for P. major and $N_b$ (Fig. 4). Reproductive output decreased as the number of P. major in a plot at the start of the season increased, suggesting intraspecific competition. Multiple regression was then used to determine the relationship between $R_0$ for P. major and $N_b$ (for P. major) controlling for $N_b$ (for H. destructor) (and $R_0$ and $N_b$ [for H. destructor] controlling for $N_b$ [for P. major]). The partial regression coefficient for $R_0$ regressed against $N_b$ (for P. major) was significant ($b = -1.32 \pm 0.117, t = 11.21, P < 0.001$), indicating intraspecific competition. Because the slope of the regression line was significantly less than $-1$ ($t = 2.69, df = 21, P < 0.01$), this situation did not match contest competition (Var-
ley et al. 1975). Instead, there seems to have been overcompensation; the decrease in individual output more than compensates for the increase in density, leading to a decrease in total reproductive output. Overcompensation is also evident from a comparison of numbers in the different treatments between the start and end of the 1997 season (Table 1). Finally, the partial regression coefficient for $R_0$ regressed against $N_b$ (for $H. destructor$) was not significant ($b = 0.034 \pm 0.082$, $t = 0.42$, $P > 0.05$), indicating that interspecific competition is not affecting $P. major$ over this period.

The relationship between $R_0$ and both $N_b$ (for $H. destructor$) and $N_b$ (for $P. major$) also was investigated for $H. destructor$ with multiple regression. The partial regression coefficient for $R_0$ regressed against $N_b$ (for $H. destructor$) revealed a significant negative slope ($b = -0.675 \pm 0.135$, $t = -5.01$, $P < 0.001$), with reproductive output decreasing as $H. destructor$ numbers in the preceding sampling date increased (Fig. 5a). Therefore, intraspecific competition affected the reproductive output of $H. destructor$. Intraspecific competition involves undercompensation because $b$ is significantly greater than a slope of $-1$ ($t = 2.41$, df = 20, $P < 0.05$). The change in reproductive output was therefore insufficient to compensate for the density changes. The partial regression coefficient for $R_0$ regressed against $N_b$ (for $P. major$) also had a significant negative slope ($b = -0.869 \pm 0.193$, $t = -4.50$, $P < 0.001$) because reproductive output of $H. destructor$ decreased as $P. major$ numbers in the preceding sampling date increased (Fig. 5b). Therefore, interspecific as well as intraspecific competition limited the reproductive output of $H. destructor$. This helps to account for the predominance of $P. major$ in most plots by the end of the season (Table 1).

The abundance patterns of $P. major$ and $H. destructor$ in pasture adjacent to the plots at Broadford during the 1996 and 1997 seasons are shown in Fig. 6. During the 1996 season, patterns of earth mite abundance were similar to those found at Yanakie, Derrimut, and Ballarat during 1995 (Fig. 1). The abundance of $P. major$ was relatively low and constant throughout the season, whereas $H. destructor$ numbers peaked at the end of the season just before diapause. However, there was a different pattern in 1997. At the start of the season, $H. destructor$ numbers were almost five times higher than those of $P. major$. The abundance of $H. destructor$ then decreased dramatically during July and August, with a concomitant increase in $P. major$ numbers. The higher relative abundance of $P. major$ matches patterns in the plots where the final sample was taken in September.

Fig. 5. Linear regression of reproductive output ($R_0$) of $H. destructor$ for the 1997 season versus (a) number of $H. destructor$ at the start of the season ($N_b$) and (b) number of $P. major$ at the start of the season ($N_b$). $R_0$ and the two $N_b$ measures were log$_{10}$ transformed.
The similar abundance patterns found at Yanakie, Derrimut, and Ballarat (Fig. 1) suggest that seasonal factors influence numbers of *P. major* and *H. destructor*. The significant increase of *H. destructor* at all sites at the end of the season is likely to offset the high mortality that occurs during diapause (Ridsdill-Smith 1991, Ridsdill-Smith and Annells 1997). However, the inability of *P. major* to increase in abundance when they also have a high reproductive potential (Weeks and Hoffmann 1999) suggests that *H. destructor* may have had a negative effect on *P. major* in the field because of limited resources. Experiments conducted herein confirm competitive interactions between these species and also indicate that *P. major* can have a negative impact on *H. destructor*.

During the first season at Broadford, interspecific competition was asymmetrical, with *H. destructor* having a negative effect on the reproductive rate of *P. major*. The second season at Broadford again showed an asymmetry in interspecific competition; however, *P. major* had a negative effect on the reproductive output of *H. destructor*. The predominance of *P. major* in pasture outside the plots indicates that this result was not limited to the plot environment. The reversal in competitive ability may be linked to the extremely dry winter experienced during 1997 and highlights the importance of looking at competitive interactions over a long period of time. Year-to-year variability for interspecific competition also has been found in other terrestrial organisms affected by dry conditions (Schoener 1983).

As well as indicating interspecific competition, the data also provide evidence for intraspecific competition in these earth mites. The effects of intraspecific competition could not be determined in the plots at Broadford in the first season for either *P. major* or *H. destructor*. However, in the generation following diapause, density-dependent effects were found for *P. major* but not for *H. destructor*. Density-dependent effects will not occur when eggs are in the diapause stage but juveniles may compete for food once diapause breaks, particularly because the juveniles are dependent on soil microflora (Maclennan et al. 1998). The density effects for *P. major* explain the significantly higher reproductive output for *P. major* in the mixed plots compared with the pure plots where densities were relatively higher. The relationship between density and the rate of population increase of *P. major* was characteristic of contest type competition because the population density of the mites was fairly constant. In the second season at Broadford, density dependence limited the reproductive output of both *P. major* and *H. destructor*. However, there was evidence for overcompensation in *P. major* and undercompensation in *H. destructor*.

Contest competition has been defined as involving behavioral interference (Lomnicki 1988). There is no evidence for interference in earth mites that can feed in aggregations at the adult stage (Gaull and Ridsdill-Smith 1996), although spider mites and predatory mites display aggressive behavior toward conspecifics, including mate competition and cannibalism of eggs (Croft et al. 1995). It is also possible that contest competition arises from factors other than behavioral interference. For instance, Prinkkila and Hanski (1995) explained contest-type competition in *Lucilia* from a combination of individual differences in larval growth rate as well as larval behavioral interference. In earth mites, contest competition could arise because of individual differences in growth rate or other fitness components. Evidence for large individual differences in fitness comes from data indicating that clones of *P. major* differ markedly in reproductive output across generations both temporally and spatially (Weeks and Hoffmann 1998). Nevertheless the traits, mechanisms, and resources underlying competitive interactions remain to be determined. Although
there was abundant plant material present in the plots when mites were present at high densities, it seems likely that some plants provide higher quality food than others.

Why do *P. major* and *H. destructor* coexist when there appears to be a high degree of resource overlap? One reason is that temporally fluctuating competition (both inter- and intraspecific) promotes the coexistence of competing species (Chesson and Warner 1981, Caceres 1998). The data from Broadford show that both interspecific and intraspecific competition between *P. major* and *H. destructor* exhibit such fluctuations. Moreover, the data also suggest that intraspecific and interspecific competition interact to promote coexistence because intraspecific competition was strongest within a species that was competitively superior during a season. However, we should emphasize that data were only collected for 2 yr, and information over many seasons would be needed for accurate predictions.

Although temporal variability in competitive ability may be important for coexistence, other factors also can play a role. Tilman (1994) has shown that in plants temporal fluctuations in competitive ability can result in the coexistence of many species. Coexistence can occur even on a single resource because species with sufficiently high dispersal rates persist in sites not occupied by a superior competitor. Although *P. major* and *H. destructor* have similar dispersal rates at the adult stage (A.R.W., unpublished data), they may well differ in dispersal at the diapause stage. Diapause eggs of *P. major* are laid singly, whereas those of *H. destructor* are held inside an adult’s body (Ridsdill-Smith 1997) and it seems likely that this difference will influence passive dispersal. Moreover, the time available for passive dispersal is different in the species because both *H. destructor* and *P. major* appear to produce diapause eggs earlier (Wallace 1970).

Although *P. major* and *H. destructor* often predominate earth mite assemblages, they also coexist with two other blue oat mite species, *P. falcatus* and *Penthaleus* species *x*, which can be locally abundant. On the basis of phylogenetic similarity, *P. major* would be expected to compete more intensively with *P. falcatus* and *P. sp. x* than *H. destructor*. However, this is not the case because both *P. sp. x* and *P. falcatus* use different hosts to *P. major* (Weeks and Hoffmann 1999). It is possible that suppression of this species is caused by *H. destructor*. However, if tolerance is specific to *H. destructor*, it is possible that suppression of this species will be accompanied by an increase in numbers of *P. major* or another of the blue oat mite species. Tolerance screening should therefore involve earth mites other than *H. destructor*

In conclusion, we have shown that competition occurs between *P. major* and *H. destructor*, although the extent to which competition influences the relative abundance of these species remains unknown. Because of competition, successful strategies to control one species may be thwarted by an increase in abundance of the other species.

Acknowledgments

We thank R. Woods, A. Magiafoglou, and C. Sinclair for help in setting up the Broadford field experiment; S. Ward for valuable discussion; and the International Wool Secretariat and the Grains Research and Development Corporation for providing funding for this research.

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Received for publication 9 November 1999; accepted 15 May 2000.