Exp Appl Acarol (2009) 47:133–145
DOI 10.1007/s10493-008-9198-y

Pre-adult development of *Phytoseiulus persimilis* on diets of *Tetranychus urticae* and *Tetranychus lintearius*: implications for the biological control of *Ulex europaeus*

Jamie T. Davies · John E. Ireson · Geoff R. Allen

Received: 17 June 2008 / Accepted: 26 September 2008 / Published online: 16 October 2008

Abstract Predation by the phytoseiid mite, *Phytoseiulus persimilis*, is considered a major threat to the effectiveness of biological control of gorse, *Ulex europaeus*, using *Tetranychus lintearius*. To assess this threat and to determine if the impact of *P. persimilis* on *T. lintearius* populations is comparable to its impact on *T. urticae* populations, its development and predator : prey generation time ratios were assessed. The pre-adult mortality and development time of two populations of *P. persimilis* fed on two diets, *T. urticae* and *T. lintearius*, were determined at two temperatures, 14 and 24°C. There were no significant differences in either mortality or development time between the two populations of *P. persimilis* at these temperatures. There is therefore no evidence that the two tested populations of *P. persimilis* are behaving as different strains. Similarly, diet had no significant effect on either mortality or development time at these temperatures. At 14°C the mortality of *P. persimilis* was significantly higher and development was significantly longer than at 24°C. Using pre-adult development as a surrogate for generation times, predator : prey generation time ratios were calculated between *P. persimilis* and both *T. urticae* and *T. lintearius* using data from this and other studies. The predator : prey generation time ratios between *P. persimilis* and *T. lintearius* were lower than those between *P. persimilis* and *T. urticae*. These results indicate that the impact of *P. persimilis* on *T. lintearius* populations is likely to be comparable to its impact on *T. urticae* populations. This provides further evidence that predation by *P. persimilis* is having a deleterious effect on *T. lintearius* populations and therefore reducing its effectiveness as a biological control agent for gorse.

J. T. Davies · G. R. Allen
School of Agricultural Science/Tasmanian Institute of Agricultural Research, University of Tasmania, Private Bag 54, Hobart, TAS 7001, Australia

Present Address:
J. T. Davies (✉)
Department of Primary Industries, PO Box 48, Frankston, VIC 3199, Australia
e-mail: jamie.davies@dpi.vic.gov.au

J. E. Ireson
Tasmanian Institute of Agricultural Research, University of Tasmania New Town Laboratories, 13 St Johns Ave., New Town, TAS 7008, Australia

Keywords Biological control · *Phytoseiulus persimilis* · *Tetranychus lintearius* · *Tetranychus urticae* · *Ulex europaeus* · Generation time ratio · Development · Natural enemy

Introduction

Host specific phytophagous arthropods are often introduced as biological control agents for invasive weeds. Natural enemies, including predatory arthropods, play a key role in regulating populations of many phytophagous arthropods (Berryman 1999) and are extensively utilised for the biological control of agricultural and horticultural pests. However, natural enemies may also reduce the population size and therefore the effectiveness of weed biological control agents (Goeden and Louda 1976; McFayden and Spafford-Jacob 2004).

Gorse, *Ulex europaeus* L. (Fabaceae), is a leguminous European woody shrub that has become a serious weed in many temperate regions of the world. In Australia, gorse is a weed of national significance in south-eastern Australia (Thorp and Lynch 2000). As part of an integrated management strategy, a guild of host specific biological control agents is currently being introduced to gorse in Australia (Ireson et al. 2004).

The gorse spider mite, *Tetranychus lintearius* Dufour (Acari: Tetranychidae), was introduced to Australia from New Zealand and released in 1998. This species is now established in Tasmania, Victoria, New South Wales, South Australia and Western Australia (J. E. Ireson, unpublished data). Its impact was demonstrated in a field study conducted in Tasmania (Davies et al. 2007) where the presence of *T. lintearius* colonies significantly reduced the dry weight of foliage on 3-year-old gorse bushes by approximately 37% over a period of 2.5 years from the time of initial infestation.

Natural enemies that have the potential to reduce the efficacy of *T. lintearius* have been identified on gorse in Australia (Davies et al. 2007; Ireson et al. 2003). One of these was the introduced predatory mite, *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae). This species is a specialist predator of tetranychid mites and is capable of reducing pest *Tetranychus* spp. populations below economically damaging levels (McMurtry and Croft 1997). As it is so effective, *P. persimilis* is available from biocontrol companies in many parts of the world including Australia (e.g. www.beneficialbugs.com.au). It is commonly used as a biocontrol agent of a polyphagous pest, the two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), and other pest *Tetranychus* spp. in a variety of crops (McMurtry and Croft 1997).

In a predator exclusion study conducted in the USA (Pratt et al. 2003), *T. lintearius* colonies were found to be larger and more numerous on gorse branches that had been excluded from *P. persimilis*, indicating that *P. persimilis* suppressed *T. lintearius* populations. In the same study, female adult survivorship, activity and oviposition of two populations of *P. persimilis* (a commercially produced population reared on *T. urticae* and a field population collected from *T. lintearius*) were assessed on two different *Tetranychus* prey species (*T. lintearius* and *T. urticae*). Oviposition of female *P. persimilis* was significantly higher when populations were reared on the prey *Tetranychus* species with which they were originally associated compared to *P. persimilis* populations that were reared on the prey species with which they were not originally associated. This result indicates a potential specialisation of *P. persimilis* populations to prey within the genus *Tetranychus* (Pratt et al. 2003).

The generation time ratio hypothesis predicts that predators will have little impact on the abundance of their prey in ecological systems where predators have longer generation times than their prey (Dixon et al. 1997). Conversely, the predators may have a significant impact on the abundance of their prey in systems where predators have shorter generation times than their prey. Therefore, predators with a smaller predator : prey generation time ratio (<1) may be more effective biological control agents of a particular pest arthropod than predators with a larger predator : prey generation time ratio (>1) (Dixon et al. 1997; Kindlmann and Dixon 1999a, 1999b; Mills 2006).

Diet is one factor that can have an influence on the development time of predators. Studies have previously been conducted on the development of *P. persimilis* on diets of pest *Tetranychus* spp. including *T. urticae* (e.g. Galazzi and Nicoli 1996), *T. kanzawai* Kishida (Hamamura et al. 1976) and *T. pacificus* McGregor (Perring and Lackey 1989). Escudero and Ferragut (2005) compared life history characteristics, including development time and survival, of *P. persimilis* when fed one of four different *Tetranychus* species. Predator performance on the different *Tetranychus* species varied and was particularly poor when *P. persimilis* was fed a diet of *T. evansi* Baker and Pritchard. The authors suggest that this may result in a poor ability of *P. persimilis* to control *T. evansi* in a cropping situation. The performance, including development time from egg to adult and survival, was greatly improved when *P. persimilis* was fed on *T. urticae*, *T. turkestani* Ugarov and Nikolski or *T. ludeni* Zacher.

The development time of *P. persimilis* can also vary between populations originating from different localities. Perring and Lackey (1989) established that a strain of *P. persimilis* from Israel developed from egg to adult almost half a day earlier than a strain from California, USA at 26.7°C and 73% RH. In other studies on the development of *P. persimilis*, significant differences were also found between the development time of different strains of *P. persimilis* originating from Great Britain, Southern Italy and Northern Italy (Galazzi and Nicoli 1996) and Ukraine and the former Czechoslovakia (Praslicka and Uhlik 1999).

Phytoseiulus persimilis seems to have adapted well to the cool temperate climate in the midlands of Tasmania and is now using *T. lintearius* as part of its diet (Ireson et al. 2003). It is therefore possible that the performance of *P. persimilis* collected from the field in Tasmania may significantly differ from *P. persimilis* that is commercially available from biocontrol companies. *Phytoseiulus persimilis* from the midlands of Tasmania will have undergone multiple generations at cooler temperatures whereas *P. persimilis* from biocontrol companies are continually exposed to the warmer conditions of glasshouse rearing.

Terms that are used to describe populations within a species include strain, biotype and race (Clarke and Walter 1995). Although host races are more precisely defined by Dres and Mallet (2002), these terms are often used interchangeably. Strains are considered by Clarke and Walter (1995) to be "populations with morphological, physiological, or behavioural traits that distinguish them from other con-specific populations". Therefore, according to this definition, if there were differences in the development of the two populations of *P. persimilis*, this would provide evidence that the Tasmanian field population is a separate strain to the population sourced from a biocontrol company.

The aim of this study was to determine if the development time and mortality of two populations of *P. persimilis* differ when reared on diets of *T. urticae* and *T. lintearius*. This was undertaken to confirm that *T. lintearius* is a suitable food source for *P. persimilis*, and to test if the Tasmanian field population of *P. persimilis* has diverged and can now be considered a distinct strain, differentiated by development time, compared to a commercially available glasshouse reared population. Finally, the development times of *P. persimilis* were compared to the development times of *T. urticae* and *T. lintearius* in

order to compare the generation time ratios of predator and prey as an index of their effectiveness on these prey diets. This was carried out to determine if the impact of *P. persimilis* on *T. lintearius* populations is comparable to its impact on *T. urticae* populations. The implication of these results on the effectiveness of *T. lintearius* as a biological control for gorse is discussed.

Materials and methods

All rearing and development experiments were conducted using facilities at New Town Research Laboratories (NTRL), located near Hobart, Tasmania, Australia.

Production of prey eggs

Eggs of *T. urticae* were produced for development experiments on bean plants. Young potted bean, *Phaseolus vulgaris* L. 'Redland Pioneer' (sourced from Yates, www.yates.com.au), were grown from seed until approximately 20 cm in height. A starter plant was initially infested with approximately 150 *T. urticae* of mixed stages collected from white clover, *Trifolium repens* L. (Fabaceae), growing as a weed at NTRL. Additional plants were placed adjacent to the infested plant as required until approximately 40 plants were infested. The plants were maintained for approximately 8 weeks from the time of initial infestation in a glasshouse with supplementary heating until high levels of *T. urticae* damage occurred. Additional uninfested *P. vulgaris* plants were placed within infested plants for 24 h to allow ambulatory dispersal of adult mites. These were removed and placed in a controlled temperature cabinet at 23°C and a 16 h photoperiod for approximately 24 h to allow egg laying to take place.

After this period, approximately 25 heavily infested leaves were removed and placed in a 200 ml beaker containing 150 ml of a 0.5% sodium hypochlorite solution and stirred briskly with a glass rod. The leaves were removed from the beaker and the solution containing eggs was poured through a synthetic fabric (60 micron monomesh, Dustcotech DHH consultants Pty Ltd, Bassendean, Western Australia) and carefully washed with distilled water. The filtered eggs were then removed with a fine sable hair brush. Eggs were stored on small (3 × 3 cm) pieces of filter paper on a petri dish for no more than 48 h in a 5°C refrigerator until required in experiments.

Eggs of *T. lintearius* were produced for development experiments on young gorse shoots. Fresh gorse stems were pruned from greenhouse grown gorse plants. These were trimmed to approximately 20 cm in length, all branches were cut off the lower 10 cm and branches on the upper 10 cm were lightly pruned so that remaining gorse foliage was cylindrical in shape, approximately 2 cm in diameter by 10 cm in length. The lower 10 cm of each cutting was inserted into water through a 4 mm hole in the centre of a screw top lid on a plastic vial 8 cm high and 3 cm in diameter. The cuttings (20 in total) were allowed to air dry and approximately 300 adult *T. lintearius* cultured on potted gorse plants (Ireson et al. 1999) in a glasshouse at around 20°C were added to each cutting. The tubes containing the cuttings with added mites were placed in a controlled temperature cabinet at 23°C and a 16 h photoperiod for approximately 24 h to allow egg laying to take place. The gorse cuttings were then removed from the vials of water and briskly rotated in a 200 ml beaker containing 150 ml of a 0.5% sodium hypochlorite solution. This solution, containing the eggs, was treated and stored until use using the same methodology as for *T. urticae*.

Predator populations and rearing

The two populations of *P. persimilis* used in this experiment were collected from different sources feeding on different *Tetranychus* species.

The Tasmanian population (Tas *P. persimilis*) was collected from a field site at Stonehenge, Tasmania (42°23′28″S, 147°37′10″E), from within *T. lintearius* colonies on gorse. This population had been observed feeding on *T. lintearius* for more than 18 months at the time this experiment was initiated (Ireson et al. 2003). Stonehenge is in an inland region at 300 m above sea level and the long term (1882–2004) record of annual temperature of the nearest weather station (Oatlands) ranges between a daily mean minimum temperature of 5°C and a daily mean maximum temperature of 15.4°C (Bureau of Meteorology 2005). Prior to the experiment, Tas *P. persimilis* was reared on *T. lintearius* colonies on potted gorse plants for approximately 4 weeks in an unheated laboratory at ambient temperature.

The second population was supplied by the 'Beneficial Bugs Co.' (www.beneficialbugs.com.au) and had been reared on *T. urticae* colonies on bean (*Phaseolus vulgaris*) at Richmond, NSW (NSW *P. persimilis*). Prior to the experiment, this population was reared at approximately 25°C in insectary conditions.

Eggs of both Tas and NSW *P. persimilis* populations were produced for the development experiment on detached bean leaf arenas. Bean (*P. vulgaris* 'Redland Pioneer') leaflets were detached from plants and placed upside down onto Petri plates containing 7 g/l water agar with the pedicels bent over and inserted into the agar. Numerous *T. urticae* eggs, collected as previously described, were placed onto each leaf arena. Five adult female *P. persimilis* were then placed onto each arena and these were then placed into a controlled temperature cabinet at 23°C and a 16 h photoperiod. Arenas were inspected every 2 h, adult female *P. persimilis* were replaced and all *P. persimilis* eggs present were collected and immediately placed into perspex arenas for the development experiment (see next section) with abundant prey eggs.

Determination of *Phytoseiulus persimilis* development times

In a factorial experiment, Tas and NSW *P. persimilis* were reared from egg to adult on the two diets (*T. urticae* and *T. lintearius*) in a randomised design. The experiment was conducted in two separate controlled temperature cabinets, which maintained the chosen temperatures (14 ± 0.7°C and 24 ± 0.7°C) and a daily photoperiod of 16 h. At each temperature 40 eggs of each of Tas and NSW *P. persimilis* were used. Diets consisted of abundant eggs of either *T. lintearius* or *T. urticae*, which were reared and extracted as previously described. Half of each of Tas and NSW *P. persimilis* (20) were allocated to each diet at each temperature. Rearing was conducted in arenas similar to those described by Perring and Lackey (1989). Arenas were constructed from 200 × 50 × 6 mm pieces of perspex. Fourteen tapered holes with diameters of 13 mm on top and 7 mm on the bottom were drilled in each piece of perspex to form the arenas. Arenas were sealed to prevent mite escape and allow unimpeded viewing. On the larger top hole, a microscope cover slip with a diameter of 17 mm was fixed to the perspex using a 1:8 mix of Vasoline® and beeswax. To allow airflow into the arenas, a synthetic fabric (60 micron monomesh) was fixed onto the smaller bottom hole using the same vasoline/beeswax mix.

One egg of *P. persimilis*, less than 2 h of age, was placed into each arena. Arenas were housed within 35 × 27 × 19 cm translucent lidded plastic boxes containing 2 l of

saturated NaCl solution, which maintained relative humidity at 75% at both temperatures (Winston and Bates 1960).

Development times from egg through to adult were determined by counting the number of cast skins in each arena at each observation every 12 h. Mites that died during or just after a moult were considered to have achieved the more advanced life stage.

Comparison of development of *Phytoseiulus persimilis* and prey *Tetranychus* spp.

Three searches were conducted on the CAB abstracts database between the years 1973 and 2008 to identify studies that have experimentally determined the development times of *P. persimilis*, *T. lintearius* and *T. urticae* at different temperatures. Keywords used were '*Phytoseiulus persimilis* and development and temperature' for the first search, '*Tetranychus lintearius* and development and temperature' for the second search and '*Tetranychus urticae* and development and temperature not predator' for the third search. 'Not predator' was specified in the third search to eliminate the numerous studies on predators of *T. urticae*.

From this literature, the data were pooled from all relevant studies on each species (although there was only one relevant study for *T. lintearius*). Pre-adult development times (in days) of each mite species were collated. Linear regressions were conducted for temperature versus development rate (1/development time in days) for each species (Data used for conducting the regressions is displayed in Fig. 1 a–c). Regressions yielded an equation in the form:

$$y = a + bx$$

where y = development rate, x = temperature, b = the slope of the regression line and $a = y$ intercept. The lower development thresholds of the three mite species were estimated by solving the regression equation for y (development rate) = 0. The number of day degrees required for development from egg to adult for each mite species was estimated by $1/b$. Standard errors for day degrees and lower development thresholds were calculated using the methods of Campbell et al. (1974).

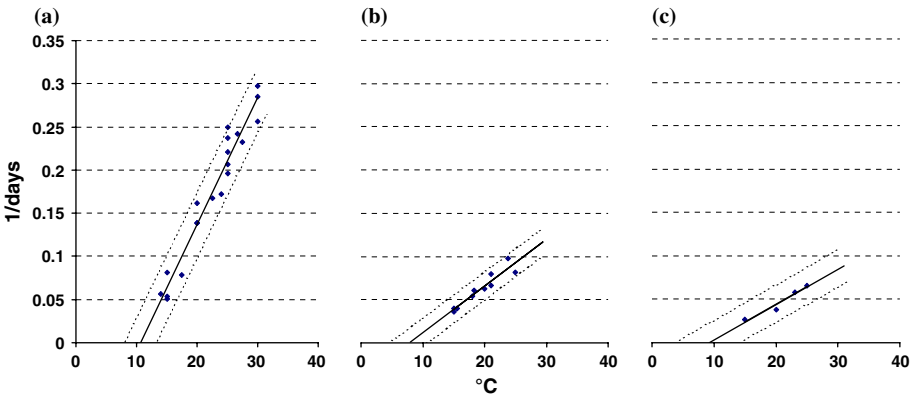

Fig. 1 Development rates (1/days) of **a** *Phytoseiulus persimilis* **b** *Tetranychus urticae* and **c** *Tetranychus lintearius*. Broken lines display 95% confidence interval. Data collated from: this study plus (**a**) Badii and McMurtry 1984; Escudero and Ferragut 2005; Galazzi and Nicoli 1996; Hamamura et al. 1976; Perring and Lackey 1989; Sabelis 1981; Toyoshima and Amano 1999; (**b**) Bounfour and Tanigoshi 2001; Carey and Bradley 1982; Herbert 1981; and (**c**) Stone 1986

The predator : prey generation time ratios were calculated using pre-adult development times as a surrogate for full generation times. Predicted development times (time in days for the development of each species from egg to adult) were determined for all three species at the standardised temperatures of 14 and 24°C by solving the reciprocal of y in the above equation when $x = 14$ and 24 respectively. The predator : prey generation time ratios between *P. persimilis*: *T. urticae* and *P. persimilis*: *T. lintearius* were calculated at both temperatures by dividing the predicted development times of *P. persimilis* by the predicted development times of *T. urticae* and *T. lintearius* respectively. Standard errors for these predicted development times were calculated using the methods of Zar (1999).

Data analysis

Statistical tests were performed using SYSTAT 10th edition. To determine if there were differences in the mortality between Tas and NSW *P. persimilis*, diets, or temperature, data on the mortality of *P. persimilis* from egg to adult were subjected to Chi-Square analyses with Yates correction factor. To determine if there were differences in the pre-adult development time between Tas and NSW *P. persimilis*, diets, or temperature, data on the development time of *P. persimilis* from egg to adult were subjected to a three factor ANOVA. Due to the pseudo-replication between temperatures, the assumption was made in these tests that the only variable differing between the two controlled temperature cabinets was temperature.

Results

Mortality of *Phytoseiulus persimilis*

There was a significant difference in mortality of both Tas and NSW *P. persimilis* across both diets in response to temperature. The mortality of *P. persimilis* from egg to adult was significantly higher at 14°C (31.3%) than at 24°C (15%) (Yates corrected $\chi^2 = 5.1$, $df = 1$, $P = 0.024$). The mortality of *P. persimilis* did not, however, significantly differ in response to diet (Yates corrected $\chi^2 = 3.9$, $df = 1$, $P = 0.19$). Similarly, there was no significant difference in mortality between the Tas and NSW populations (Yates corrected $\chi^2 = 2.3$, $df = 1$, $P = 0.13$).

From egg to adult, the highest level of mortality at 14°C was experienced by NSW *P. persimilis* on a diet of *T. lintearius* (50%). The lowest level of mortality at 14°C was experienced by Tas *P. persimilis* on a diet of *T. urticae* (20%). Similarly at 24°C, the highest level of mortality from egg to adult was also experienced by NSW *P. persimilis* on a diet of *T. lintearius* (25%). The lowest level of mortality at 24°C was experienced by both Tas and NSW *P. persimilis* on a diet of *T. urticae* (10%) (Table 1). The majority of deaths for all treatments occurred in the egg, larval and protonymph stages (Table 1). The mean mortalities independent of population, diet and temperature were 9.4% (egg), 6.2% (larvae) and 9.6% (protonymph). The deutonymph stage experienced relatively little mortality (0.8%).

Determination of development times

There was a significant difference in the development time from egg to adult in response to temperature ($F_{1,114} = 9940$, $P < 0.001$). The mean development time of *P. persimilis* from egg to adult was 17.8 days at 14°C and 5.8 days at 24°C (Table 2a, b). The development of

Table 1 Mortality of pre-adult life stages of NSW and Tas populations of *Phytoseiulus persimilis* reared on diets of *Tetranychus urticae* and *Tetranychus lintearius* at 14 and 24°C

Life stage		*T. urticae*		*T. lintearius*	
		Tas	NSW	Tas	NSW
14°C	Egg	2 (20)	4 (20)	0 (20)	4 (20)
	Larvae	2 (18)	0 (16)	2 (20)	2 (16)
	Protonymph	0 (16)	2 (16)	3 (18)	4 (14)
	Deutonymph	0 (16)	1 (14)	0 (15)	0 (10)
	Egg to adult mortality %	20	35	25	50
24°C	Egg	1 (20)	2 (20)	2 (20)	0 (20)
	Larvae	1 (19)	0 (18)	0 (18)	2 (20)
	Protonymph	0 (18)	0 (18)	1 (18)	3 (18)
	Deutonymph	0 (18)	0 (18)	0 (17)	0 (15)
	Egg to adult mortality %	10	10	15	25

Data for egg, larvae, protonymph and deutonymph are the number of deaths that occurred in each lifestage, followed by the number of live *P. persimilis* entering each stage (in parentheses)

Table 2 Mean development time (days ± SE) for pre-adult life stages of NSW and Tas populations of *Phytoseiulus persimilis* reared on diets of *Tetranychus urticae* (two-spotted spider mite) and *Tetranychus lintearius* (gorse spider mite) at 14 and 24°C

P. persimilis life stage	*T. urticae*		*T. lintearius*	
	Tas	NSW	Tas	NSW
14°C				
Egg	7.8 ± 0.07 (18)	7.6 ± 0.10 (16)	8.0 ± 0.09 (20)	8.0 ± 0.12 (16)
Larva	2.2 ± 0.12 (16)	2.5 ± 0.12 (16)	2.1 ± 0.09 (18)	2.4 ± 0.13 (14)
Protonymph	3.6 ± 0.16 (16)	3.9 ± 0.17 (14)	3.9 ± 0.17 (15)	3.9 ± 0.16 (10)
Deutonymph	3.9 ± 0.14 (16)	3.9 ± 0.15 (13)	3.8 ± 0.14 (15)	3.8 ± 0.08 (10)
Egg to adult	17.5 ± 1.4 (16)	17.9 ± 1.2 (13)	17.7 ± 1.1 (15)	18.1 ± 1.3 (10)
24°C				
Egg	2.5 ± 0.05 (19)	2.5 ± 0.06 (18)	2.3 ± 0.10 (18)	2.4 ± 0.06 (20)
Larva	0.6 ± 0.05 (18)	0.6 ± 0.05 (18)	0.7 ± 0.06 (18)	0.6 ± 0.05 (18)
Protonymph	1.4 ± 0.08 (18)	1.5 ± 0.04 (18)	1.4 ± 0.08 (17)	1.4 ± 0.07 (15)
Deutonymph	1.6 ± 0.07 (18)	1.4 ± 0.08 (18)	1.3 ± 0.07 (17)	1.2 ± 0.08 (15)
Egg to adult	6.1 ± 0.6 (18)	6.0 ± 0.6 (18)	5.6 ± 0.6 (17)	5.6 ± 0.6 (15)

The numbers in parentheses represent the number of individuals comprising the mean

P. persimilis from egg to adult did not significantly differ in response to diet ($F_{1,114} = 1.3$, $P = 0.25$). Similarly, there was no significant difference in the development time from egg to adult between the Tas and NSW *P. persimilis* populations ($F_{1,114} = 3.0$, $P = 0.09$). There were significant interactions between temperature and both diet and population (temperature × population: $F_{1,114} = 4.65$, $P = 0.03$; temperature × diet: $F_{1,114} = 5.8$, $P = 0.02$) but no significant interactions were evident between diet and population or all three factors (diet × population: $F_{1,114} = 0.14$, $P = 0.71$; temperature × diet × population: $F_{1,114} = 0.14$, $P = 0.71$).

Table 3 Development times (days from egg-adult), predator : prey generation time ratios (GTR) (using pre-adult development as a surrogate for full generation times), day degrees (DD) required to complete development from egg to adult and lower development thresholds at 14°C and 24°C for *Phytoseiulus persimilis* (predator), *Tetranychus urticae* (prey) and *T. lintearius* (prey)

	Phytoseiulus persimilis	*Tetranychus urticae*	*Tetranychus lintearius*
Equation	$y = 0.0146x - 0.1549$	$y = 0.0054x - 0.0419$	$y = 0.0041x - 0.037$
R^2	0.9491	0.8929	0.9557
Days (±SE) from egg-adult at 14°C[1]	20.2 ± 5.62	29.7 ± 1.44	49.0 ± 1.26
Predator : prey GTR at 14°C[3]	n/a	0.68	0.41
Days (±SE) from egg-adult at 24°C[2]	5.12 ± 0.90	11.4 ± 1.29	16.3 ± 0.61
Predator : prey GTR at 24°C[3]	n/a	0.45	0.31
DD[4] to complete development	68.5 ± 3.75	185.2 ± 22.6	243.9 ± 36.7
Lower development threshold	10.6 ± 1.2°C	7.8 ± 1.3°C	9.0 ± 1.2°C

[1] Calculated by solving y on equation when $x = 14$

[2] Calculated by solving y on equation when $x = 24$

[3] Calculated by dividing prey (either *T. urticae* or *T. lintearius*) development time (egg to adult) by predator (*P. persimilis*) development time (egg to adult)

[4] Day degrees (±SE) above lower development threshold

Comparison of development rates and generation times of *Phytoseiulus persimilis*, *Tetranychus urticae* and *Tetranychus lintearius*

Plots of the development rates (1/days) are provided for *P. persimilis* (Fig. 1a), *T. urticae* (Fig. 1b) and *T. lintearius* (Fig. 1c). From egg to adult, *P. persimilis* had the most rapid development rate and the lowest number of day degrees (68.5 DD) to complete development (Table 3, Fig. 1). For *T. urticae*, a slower development rate resulted in the number of day degrees required to complete development being more than double that of *P. persimilis* (185.2 DD). *T. lintearius* had the slowest development rate with the number of day degrees (243.9 DD) required to complete development 3.5 times that of *P. persimilis*.

The lower development threshold for *P. persimilis* (10.6°C) was higher than either of its prey species. The lower development threshold for *T. lintearius* (9°C) was higher than that for *T. urticae* (7.8°C) (Table 3). However, when the 95% confidence intervals are compared there is no distinguishable difference between the lower development thresholds of the three species (Fig. 1).

The predator : prey generation time ratios were much less than one for both prey species at both 14 and 24°C and consistently higher between *P. persimilis* and *T. urticae* than between *P. persimilis* and *T. lintearius*. At 14°C, *P. persimilis* will complete its development in almost half the time of *T. urticae* and less than half the time of *T. lintearius*. At 24°C, *P. persimilis* will complete its development in less than half the time of *T. urticae* and less than a third of the time of *T. lintearius* (Table 3).

Discussion

The mortality and development of both populations of *P. persimilis* were similar on both diets. These results confirm that *T. lintearius* is a suitable prey species for *P. persimilis*.

This result supports previous studies where *P. persimilis* has been observed to build up in large numbers under field conditions and suppress *T. lintearius* populations (Ireson et al. 2003; Pratt et al. 2003).

The mortality and development of both Tas and NSW *P. persimilis* were also similar, indicating that the performance of the Tasmanian field population of *P. persimilis* is comparable to the commercially available population from NSW. As no difference in physiological traits could be detected, there is no evidence in this study that the two populations are behaving as different strains according to Clarke and Walters (1995) definition.

Predators with a smaller predator : prey generation time ratio (<1) may be more effective biological control agents of a particular pest arthropod than predators with a larger predator : prey generation time ratio (>1) (Dixon et al. 1997). In this study, we applied the generation time ratio hypothesis to a predator of a weed biological control agent rather than a predatory biological control agent of a pest arthropod. However, as it is a typical predator : prey relationship, the generation time ratio hypothesis should still apply.

It has been shown in previous studies that *P. persimilis* has a significant impact on the abundance of *T. urticae* and is indeed a very effective biological control agent of this species (McMurtry and Croft 1997). Compared to *T. urticae*, *T. lintearius* has a relatively longer generation time and therefore the predator : prey generation time ratio is even smaller. Therefore, in accordance with the generation time ratio hypothesis (Dixon et al. 1997), it is likely that the impact of *P. persimilis* on *T. lintearius* populations will be as great as or even greater than its impact on *T. urticae* populations. Other life history traits are also important factors that determine the efficacy of natural enemies (Bellows et al. 1992). In addition to a rapid development time compared to their prey, predatory mites in the genus *Phytoseiulus* also display other life history characteristics that contribute to their ability to rapidly suppress *Tetranychus* populations (McMurtry and Croft 1997), such as a density-dependent response to spider mites, a high prey consumption rate and a high fecundity. Pratt et al. (2003) has reported high levels of fecundity for *P. persimilis* on diets of both *T. lintearius* and *T. urticae* (4.17 and 4.10 eggs per female per day respectively).

In the Tasmanian midlands, it was demonstrated that *T. lintearius* can have a significant impact on gorse growth and therefore has the potential to be a useful biological control agent (Davies et al. 2007). This reduction in growth was measured over 2.5 years from the initial establishment of *T. lintearius* at the site. Two predators, the predatory ladybird beetle, *Stethorus* sp. and *P. persimilis*, were first recorded at the site 8–10 months respectively after the establishment of *T. lintearius*. No quantitative data on the impact of the predators on *T. lintearius* was obtained in this study. It is therefore unknown if the impact of *T. lintearius* would have increased significantly in the absence of the predation. However, it is possible that the maximum level of control that predation could have exerted in this study (Davies et al. 2007) would not have been evident until after the trial was concluded as predator population densities may not have reached maximum levels until then. Surveys by Ireson et al. (2003) concluded that *P. persimilis* is widespread in *T. lintearius* populations throughout much of Tasmania and have associated this predator with the destruction of entire colonies of *T. lintearius*. This association is supported by predator exclusion studies in the USA by Pratt et al. (2003), who showed that predation by *P. persimilis* can significantly reduce the size and number of *T. lintearius* colonies.

Predation of *T. urticae* by *P. persimilis* can result in localised extinction in an enclosed, protected environment such as a glasshouse and is therefore a very effective biological control agent of *T. urticae* in this situation. However, in a natural environment prey

dispersal, and asynchrony in predator and prey populations will result in a patchy equilibrium, with alternating prey overpopulation and localised extinctions occurring (Pels and Sabelis 1999). Presumably, similar dynamics between *T. lintearius* and *P. persimilis* will occur and asynchronous predator and prey populations will develop throughout gorse populations. This may result in a low occurrence of the higher damage levels measured by Davies et al. (2007), with low levels of patchy damage to gorse becoming the norm once predator and prey populations stabilise. Evidence that this is occurring in Tasmania is provided by the widespread but localised damage that is now being observed at sites around the state. This contrasts with the widespread and highly damaging outbreaks of *T. lintearius* that were observed during the first 2 or 3 years following its initial release into the state (J. E. Ireson, personal communication).

Two other biological control agents have established on gorse in Australia, but the impacts of both appear to be limited. The gorse seed weevil, *Exapion ulicis* Forster (Coleoptera: Brentidae), attacks seed within gorse pods, but a large proportion escapes attack (Davies et al. 2008). The gorse thrips, *Sericothrips staphylinus* Haliday (Thysanoptera: Thripidae), performed well in a glasshouse study (Davies et al. 2005), however, its impact in the field may be limited due to host phenological factors (Ireson et al. 2008). The current study provides further evidence that predation by *P. persimilis* is having a deleterious effect on *T. lintearius* populations. It is therefore likely that the level and frequency of damage to gorse by *T. lintearius* will be lower than would otherwise have been recorded in the absence of *P. persimilis*. Although the combination of these agents is having an impact, additional agents that further suppress the growth and seed production of gorse may be required if biological control is to be considered an important long-term component of an integrated management strategy for gorse.

Acknowledgements We thank A.F.G. Dixon (University of East Anglia, Norwich, UK) and Marilyn Steiner (NSW Agriculture) for experimental advice, Andy Ryland (Beneficial Bug Co., NSW) for providing the NSW population of *P. persimilis*, and Richard Holloway and Wade Chatterton (Tasmanian Institute of Agricultural Research) for technical support. Funding support was provided by the CRC for Australian Weed Management.

References

Badii MH, McMurtry JA (1984) Life history of and life table parameters for *Phytoseiulus longipes* with comparative studies on *P. persimilis* and *Typhlodromus occidentalis* (Acari: Phytoseiidae). Acarologia 25:111–123

Bellows TS, Van Driesche RG, Elkington JS (1992) Life table construction and analysis in the evaluation of natural enemies. Annu Rev Entomol 37:587–614. doi:10.1146/annurev.en.37.010192.003103

Berryman AA (1999) The theoretical foundations of biological control. In: Hawkins BA, Cornell HV (eds) Theoretical approaches to biological control. Cambridge University Press, UK, pp 3–21

Bounfour M, Tanigoshi LK (2001) Effect of temperature on development and demographic parameters of *Tetranychus urticae* and *Eotetranychus carpini* borealis. Ann Entomol Soc Am 94:400–404. doi:10.1603/0013-8746(2001)094[0400:EOTODA]2.0.CO;2

Bureau of Meteorology (2005) Bureau of Meteorology website, Tasmanian weather records (www.bom.gov.au). Accessed December, 2005

Campbell A, Frazer BD, Gilbert N, Gutierrez AP, Mackauer M (1974) Temperature requirements of some aphids and their parasites. J Appl Ecol 11:431–438. doi:10.2307/2402197

Carey JR, Bradley JW (1982) Development rates, vital schedules, sex ratios, and life tables for *Tetranychus urticae, T.* turkestani and *T. pacificus* on cotton. Acarologia 23:333–345

Clarke AR, Walter GH (1995) "Strains" and the classical biological control of insect pests. Can J Zool 73:1777–1790. doi:10.1139/z95-210

Davies JT, Ireson JE, Allen GR (2005) The impact of gorse thrips, ryegrass competition, and simulated grazing on gorse seedling performance in a controlled environment. Biol Control 32:280–286. doi:10.1016/j.biocontrol.2004.10.007

Davies JT, Ireson JE, Allen GR (2007) The impact of the gorse spider mite, *Tetranychus lintearius*, on the growth and development of gorse, *Ulex europaeus*. Biol Control 41:86–93. doi:10.1016/j.biocontrol.2006.12.014

Davies JT, Ireson JE, Allen GR (2008) The phenology and impact of the gorse seed weevil, *Exapion ulicis*, on gorse, *Ulex europaeus*, in Tasmania. Biol Control 45:85–92. doi:10.1016/j.biocontrol.2008.01.009

Dixon AFG, Hemptinne JL, Kindlmann P (1997) Effectiveness of ladybirds as biological control agents: patterns and processes. Entomophaga 42:71–83. doi:10.1007/BF02769882

Dres M, Mallet J (2002) Host races in plant-feeding insects and their importance in sympatric speciation. Philos Trans R Soc Lond B Biol Sci 357:471–492. doi:10.1098/rstb.2002.1059

Escudero LA, Ferragut F (2005) Life history of predatory mites *Neoseiulus californicus* and *Phytoseiulus persimilis* (Acari: Phytoseiidae) on four spider mite species as prey, with special reference to *Tetranychus evansi* (Acari: Tetranychidae). Biol Control 32:378–384. doi:10.1016/j.biocontrol.2004.12.010

Galazzi D, Nicoli G (1996) Comparative study of strains of *Phytoseiulus persimilis* 1. Development and adult life. Bollettino dell'Istituto di Entomologia 'Guido Grandi' della Universita degli Studi di Bologna 50:215–231

Goeden RD, Louda SM (1976) Biotic interference with insects imported for weed control. Annu Rev Entomol 21:325–342. doi:10.1146/annurev.en.21.010176.001545

Hamamura T, Shinkaji N, Ashihara A (1976) The relationship between temperature and developmental period, and oviposition of *Phytoseiulus persimilis*. Bull Fruit Tree Res Stn 1:117–125

Herbert HJ (1981) Biology, life tables and innate capacity for increase of the two spotted spider mite, *Tetranychus urticae*. Can Entomol 113:371–378

Ireson JE, Gourlay AH, Kwong RM, Holloway RJ, Chatterton WS (1999) Progress on the rearing, release and establishment of the gorse spider mite, Tetranychus lintearius Dufour, for the biological control of gorse in Australia. In: Bishop AC, Boersma M, Barnes CD (eds) Proceedings of the 12th Australian Weeds Conference, Tasmanian Weed Society, Devonport, pp 320–324

Ireson JE, Gourlay AH, Kwong RM, Holloway RJ, Chatterton WS (2003) Host specificity, release and establishment of the gorse spider mite, *Tetranychus lintearius* Dufour (Acari: Tetranychidae), for the biological control of gorse, *Ulex europaeus* L. (Fabaceae), in Australia. Biol Control 26:117–127. doi:10.1016/S1049-9644(02)00128-7

Ireson JE, Kwong RM, Gourlay AH, Davies JT, Chatterton WS, Holloway RJ (2004) Progress on the biological control of gorse (*Ulex europaeus*) in Australia. In: Cullen JM, Briese DT, Kriticos DJ, Lonsdale WM, Morin L, Scott JK (eds) Proceedings of the XI International Symposium on Biological Control of Weeds. CSIRO Entomology, Canberra, pp 415–418

Ireson JE, Holloway RJ, Chatterton WS (2008) Phenology and development of the gorse thrips, *Sericothrips staphylinus* Haliday (Thysanoptera: Thripidae), a biological control agent for gorse, *Ulex europaeus* L. (Fabaceae), in Tasmania. Biol Control 45:64–71. doi:10.1016/j.biocontrol.2007.10.019

Kindlmann P, Dixon AFG (1999a) Generation time ratios–determinants of prey abundance in insect predator-prey systems. Biol Control 16:133–138. doi:10.1006/bcon.1999.0754

Kindlmann P, Dixon AFG (1999b) Strategies of aphidophagous predators: lessons for modelling insect predator–prey dynamics. J Appl Entomol 123:397–399. doi:10.1046/j.1439-0418.1999.00390.x

McFayden RC, Spafford-Jacob H (2004) Insects for the biological control of weeds: Predicting parasitism levels in the new country. In: Cullen JM, Briese DT, Kriticos DJ, Lonsdale WM, Morin L, Scott JK (eds) Proceedings of the XI International Symposium on Biological Control of Weeds. CSIRO Entomology, Canberra, pp 135–140

McMurtry JA, Croft BA (1997) Life-styles of Phytoseiid mites and their role in biological control. Annu Rev Entomol 42:291–321. doi:10.1146/annurev.ento.42.1.291

Mills NJ (2006) Accounting for differential success in the biological control of homopteran and lepidopteran pests. N Z J Ecol 30:61–72

Pels B, Sabelis MW (1999) Local dynamics, overexploitation and predator dispersal in an acarine predator–prey system. Oikos 86:573–583. doi:10.2307/3546662

Perring TM, Lackey LJ (1989) Temperature and humidity effects on mortality and pre-adult development of two *Phytoseiulus persimilis* strains (Acari: Phytoseiidae). Int J Acarol 15:47–52

Praslicka J, Uhlik V (1999) Influence of temperature and relative humidity on the development of predatory mite *Phytoseiulus persimilis*. Acta fytotechnica et zootechnicha 4:11–113

Pratt PD, Coombs EM, Croft BA (2003) Predation by Phytoseiid mites on *Tetranychus lintearius*, an established weed biological control agent of gorse (*Ulex europaeus*). Biol Control 26:40–47. doi:10.1016/S1049-9644(02)00114-7

Sabelis MW (1981) Biological control of two-spotted spider mites using phytoseiid predators. Agricultural research report 910. Pudoc, Wageningen, The Netherlands

Stone C (1986) An investigation into the morphology and biology of *Tetranychus lintearius* Dufour (Acari: Tetranychidae). Exp Appl Acarol 2:173–186. doi:10.1007/BF01213760

Thorp JR, Lynch R (2000) The determination of weeds of national significance. National Weeds Strategy Executive Committee, Launceston

Toyoshima S, Amano H (1999) Comparison of development and reproduction in offspring produced by females of *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) under two prey conditions. Appl Entomol Zool (Jpn) 34:285–292

Winston PW, Bates DH (1960) Saturated solutions for the control of humidity in biological research. Ecology 41:232–237. doi:10.2307/1931961

Zar JH (1999) Biostatistical analysis. Prentice Hall, New Jersey