

Population dynamics of an introduced biological control agent for gorse in New Zealand: a simulation study

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Abstract. The gorse spider mite, *Tetranychus lintearius* was introduced into New Zealand from the United Kingdom in 1989 for the control of gorse. Although now widely distributed throughout the country, it did not establish in two particular geographic locations which have mild, wet winters. This paper presents a temperature-driven population model of the gorse spider mite which was developed in order to increase our understanding of the population dynamics of the mite and to determine the role of temperature in the successful establishment of the mite. Aspects of the life cycle of gorse spider mite were determined in the laboratory and incorporated, with appropriate assumptions, into the framework of a deterministic population model. These aspects were temperature-dependent development, temperature-dependent fecundity, temperature-dependent survival and sex ratio. Using regional temperature profiles the model was used to predict the number of generations, the relative population growth and the overwintering behaviour of the mite in different geographic regions of New Zealand. The results are discussed with respect to differences in establishment success.

Introduction

Much effort has gone into characterizing the features of biocontrol agents that enhance their chances of successful establishment and control. For biological weed control with insect agents, establishment seems to be improved by selecting agents with a high intrinsic rate of increase (Crawley 1986; Lawton 1990), which tends to be associated with small body sizes and short generation times. Rapid growth of founder populations reduces the likelihood of extinctions due to stochastic effects. The selection of a multivoltine spider mite as a potential biocontrol agent of gorse, *Ulex europaeus* L., Fabaceae (Leguminosae: Genisteae) (Hill 1983), would therefore be expected to have a high possibility of success.

The gorse spider mite, *Tetranychus lintearius* Dufour (Acari: Tetranychidae), was introduced into New Zealand from Cornwall, England in 1989. The mites established well in most parts of New Zealand but, despite repeated introductions over three years, they established poorly in the northern half of the North Island and on the West Coast of the South Island. These regions have warm winters and high rainfall, and research has shown that rainfall is a major factor

reducing survival of the mites (Hill *et al.* 1993; Millar 1993). Apparently, heavy rainfall during periods of warm temperatures, causes entanglement and death of the mites that are dispersed throughout the web. However, the role of temperature in mite survival and establishment is unresolved. The gorse spider mite is difficult to study because of its small size, ability to disperse over large distances, colonial behaviour (with huge numbers in any one colony) and, in its natural environment, sudden local extinctions due to predation by the coccinellid beetle *Stethorus bifidus* (Peterson 1993).

A temperature-driven population model of *T. lintearius* has been developed in order to increase our understanding of its population dynamics in different geographic regions of New Zealand. In particular, the model was developed to explain the establishment difficulties with the United Kingdom strain in some regions and, ultimately, to compare the population dynamics of the original (UK strain) with new strains of the mite introduced from Portugal and Spain. We were concerned in this study only with establishment and not the efficacy of the mite and we did not attempt to predict absolute population density but to use the model comparatively. Specific questions

that we asked were: (i) how many generations of the mite are there in warm North Island sites and cooler South Island sites; (ii) what is the overwintering behaviour of the mite in different regions; (iii) does oviposition continue throughout the winter in mild temperatures; and (iv) what is the relative population growth in different regions?

Gorse spider mite population-model framework

The gorse mite population model is based on the phenological framework of a single-generation, insect-population model (Logan and Amman 1986). The gorse-spider-mite phenology model described in Hayes *et al.* (1994) has been expanded into a full population model for multiple generations. The model contains separate age classes for eggs, nymphs, pre-oviposition females, ovipositing females and 'over-wintered' females. Males are not included in the model and are assumed to be in sufficient numbers to effect maximal insemination of the females. The numbers of individuals in any age class are the result of recruitment from oviposition or completion of development of the previous age-class, minus the numbers leaving the age class due to completion of stage development or mortality. The model operates on a time-step of one hour. Temperatures during each time-step are assumed to be constant and determined either from direct measurements of gorse spine temperatures, using a data logger, or simulated from daily maximum and minimum ambient temperatures and then adjusted with a correlation equation for gorse spine temperatures. An assumption that is used throughout the model is that the increments of development, survival and fecundity accumulated during each time-step can be summed to determine total development, survival or fecundity in a fluctuating temperature regime.

Modelling diurnal temperature cycles and gorse plant temperatures

Sensitivity analysis showed that the output from the phenology model is sensitive to small changes in temperature (Hayes *et al.* 1994) so temperature inputs to the model needed to be measured as accurately as possible. Gorse plant temperatures, determined with a Campbell CR 10 data logger during March and April at Lincoln, were on average 3°C higher during the day

and 1°C cooler at night than ambient temperatures. A regression equation (Table 1.) was used to predict both daily maximum and minimum plant temperatures from maximum and minimum ambient temperatures, recorded within a Stevenson screen. A temperature simulator (Rabbinge 1976), using a combination of a sine-wave model for day-time temperatures and an exponential curve for night-time temperatures, was used to simulate hourly temperatures from maximum and minimum daily temperatures.

Model development

The process of model development involved the following steps: (i) determination of developmental rate, fecundity, mortality and sex ratio under laboratory conditions at constant temperatures; (ii) fitting of statistical or analytical models to describe temperature-dependent relationships and inserting these into the model framework; (iii) validation of parts of the model with independently-derived field-, glasshouse- or laboratory-data; and (iv) applications.

Laboratory experiments

When working with adult mites, the experimental unit was either a freshly-cut gorse stem, trimmed to leave one lateral shoot and held in a sealed vial of water, or excised lateral shoots, placed on moist cotton wool inside plastic containers. For work on the juvenile stages, each gorse shoot was trimmed to a single spine. The gorse shoots or spines were placed in constant temperature cabinets (in a long-day regime, 16:8, L:D) at constant temperatures ranging from 6-27°C. Humidity was not controlled in the experiments but shoots were kept within closed containers and the relative humidity was >80%.

The fecundity of 30 adult females from a laboratory culture was determined by keeping individual females on separate gorse stems. Fecundity was measured at constant temperatures of 15, 18, 20, 25, and 27°C. There was no age-dependent effect on fecundity so the average daily fecundity per female was calculated from the total fecundity divided by the oviposition period. This experiment also yielded information on longevity of the adults.

In a later experiment, fecundity and survival at temperatures of 6, 8, 10, 11 and 12°C were determined over a six-week period, with mixed-age adult females obtained from the field in summer, using five females per spine. The fecundity and survival of overwintered

females was determined at temperatures of 8 and 20°C (1994) and 10, 12 and 15°C (1995) using female *T. lintearius* adults that were collected from the field in late winter, before egg-laying had commenced. The proportional mortality of eggs and nymphs at constant temperatures was determined both from the development-rate experiments and, separately, at 6 and 10°C.

Temperature-dependent relationships

The developmental rates of the different stages of the mites (defined as the reciprocal of time to complete stage-development) were strongly temperature-dependent and modelled with either a linear or power function for proportional development per day against temperature (Hayes *et al.* 1994). The present version of the model was simplified by treating all the juvenile stages as a single stage. A distinct pre-oviposition period was observed, the duration of which was also strongly temperature-dependent. The oviposition period was long (>40 days at temperatures between 15°C and 20°C) and was modelled in a similar way to development. The models for the temperature-dependent development rate of each stage are given in Table 1.

A linear model was fitted between 15 and 25°C for daily fecundity per female (collected in summer) giving a threshold of 10.3°C. Data at 27°C were not used in the regression analysis as they appeared to be outlying points. Rates of oviposition at 10 and 11°C (0.051 and 0.188 eggs/female/day) were consistent with this model, as was the absence of oviposition at 6 and 8°C, but the oviposition rate at 12°C was inexplicably lower than at 10 and 11°C (Fig. 1).

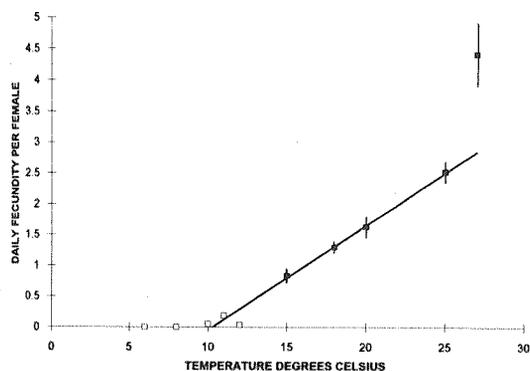


Fig. 1. Mean (and 95% confidence limits) of daily fecundity per female of *T. lintearius*: closed squares = determined throughout lifespan; open squares = determined over six-week period with mixed-age female *T. lintearius* collected in summer. Unbroken line = linear model fitted to fecundity.

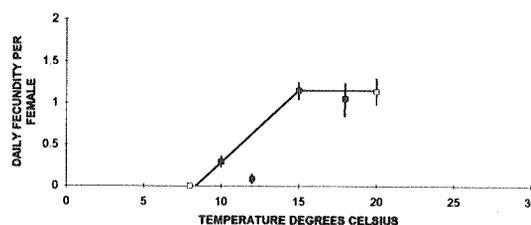


Fig. 2. Mean (and 95% confidence limits) of daily fecundity per female of overwintered *T. lintearius*. Open squares = collected winter 1994; closed squares = collected winter 1995; unbroken line = model fitted to fecundity.

Daily fecundity of females, collected in winter, appeared to be linear at low temperatures and reach a plateau, with maximum oviposition at 15°C (Fig. 2). Fecundity was determined over at least three weeks, once it reached a steady rate, usually after the first week. Oviposition at 12°C was lower than at 10°C, was irregular over time and mites suffered high mortality. Data at 12°C were therefore excluded from the analysis. The linear part of the model for daily fecundity of overwintered females, had a lower temperature threshold for oviposition (8.6°C) than females collected in summer, but the slopes were similar.

The survival of ovipositing mites was high during the first 50 days at moderate temperatures followed by an abrupt drop in survival presumably due to ageing. Proportional mortality per day was determined from the early part of the lifespan and ageing was treated separately (see above). The relationship between proportional mortality per day and temperature for females collected in summer and winter is shown in Fig. 3. Adult females collected in winter suffered much lower mortality in the low temperature range. The range of temperatures for optimum survival of eggs was similar to that for summer-collected females but nymphs suffered little mortality at temperatures above 6°C (Table 1).

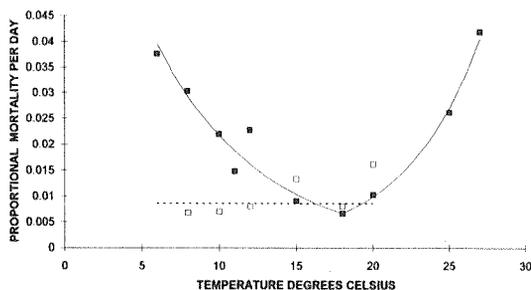


Fig. 3. Proportional mortality per day of summer (closed squares) and overwintered (open squares) female *T. lintearius*.

Independent validation

Small-scale validation showed that the model predicted the duration of the egg period accurately (Hayes *et al.* 1994). Further validation of simulated phenology was carried out with data derived from marked colonies of mites at two sites near Lincoln. Thirty colonies of 200 overwintered adults, collected from near Lincoln were established on mite-free gorse bushes at Fereday's Island and North Rakaia on 9 September 1993. The change in population structure of the colonies was determined by removing three whole colonies at approximately three week intervals and counting numbers of each mite stage in the laboratory. The same events were simulated, using as inputs 200 overwintered females and maximum and minimum temperatures from the closest meteorological station (30 km distant) which were then adjusted to give gorse plant temperatures. Despite predation by *S. bifidus*, causing extinction of mite populations at 118 days and 140 days after release, the field data clearly showed two generations of eggs and nymphs between mid-September and the end of January. The timing of these generations was simulated accurately by the model (Fig. 4).

The relationship for temperature-dependent daily fecundity was the same as published data on fecundity rates at constant temperatures: 0.835 eggs per female per day at 15°C (Millar 1993) and 2.3 eggs per female per day at 23°C (Stone 1986). Simulated fecundity and survival were also compared to data collected in a fluctuating temperature regime (mean daily minima 7°C, mean daily maxima 23°C) in a glasshouse (Millar 1993). Cumulative egg production averaged over 10 replicates of 10 adult females for 10 days was 83.4 compared to 86.02 simulated. The average survival after 10 days was 86% compared to 81.5% simulated. No independent validation of egg production and survival for overwintered females has yet been carried out.

Applications*Regional variation in phenology*

The model was used to simulate the number of mite generations in different geographical locations of New Zealand between spring and autumn, using maximum and minimum daily climatology data (National

Table 1. The statistical models used in the simulation model for proportional development per day (D), fecundity per female per day (F) and proportional mortality per day (M), as a function of temperature (T).

Eggs	$D = 4.1368 \cdot 10^{-5} \cdot T^{2.6199}$ $R^2 = 0.964$, df 1,719; $p < 0.001$
Nymphs	$D = 8.167 \cdot 10^{-5} \cdot T^{2.243}$ $R^2 = 0.937$, df 1,104; $p < 0.001$
Pre-oviposition period	$D = 6.352 \cdot 10^{-5} \cdot T^{2.748}$ $R^2 = 0.861$, df 1,85; $p < 0.001$
Sex ratio of emerging adults	females:males 5.35:1, n = 108
Oviposition period 'summer' females	$D = 1.226 \cdot 10^{-2} \cdot T - 1.534 \cdot 10^{-3}$, $R^2 = 0.54$, df 1,3; $p = 0.16$
Oviposition period 'winter' females	$D = 1.226 \cdot 10^{-2} \cdot T - 1.534 \cdot 10^{-3}$, $R^2 = 0.54$, df 1,3; $p = 0.16$
Fecundity of 'summer' females	$F = 0.1704 \cdot T - 1.754$, $R^2 = 0.695$, df 1,96; $p < 0.001$, Threshold = 10.3°C
Fecundity of 'winter' females: below 15°C, above 15°C,	$F = 0.1744 \cdot T - 1.465$, $R^2 = 0.84$, df 1,37; $p < 0.001$, Threshold = 8.6°C $F = 0.802$
Egg mortality	$M = 0$ between temperatures 13.8°C and 25°C $M = 0.0065 \cdot T - 0.163$, temperatures above 25°C $M = 0.038 - 0.0028 \cdot T$, temperatures below 13.8°C
Nymph mortality	$M = 0.008$ at temperatures below 18.9°C $M = 0.0028 \cdot T - 0.045$, temperatures above 18.9°C
'Summer' female mortality	$M = 1.79 \times 10^{-4} \cdot e^{0.201T}$, above 18°C $M = 9.69 \times 10^{-4} \cdot e^{-0.149T}$, below 18°C
'Winter' female mortality	$M = 1.79 \times 10^{-4} \cdot e^{0.201T}$, above 18°C $M = 0.0086$, below 18°C
Gorse plant temperature (gmin, gmax) prediction from ambient (smin, smax)	$gmin = 1.039 \cdot smin - 1.111$ $R^2 = 0.99$, df 1,33; $p < 0.001$ $gmax = 1.017 \cdot smax + 2.82$ $R^2 = 0.83$, df 1,34; $p < 0.001$

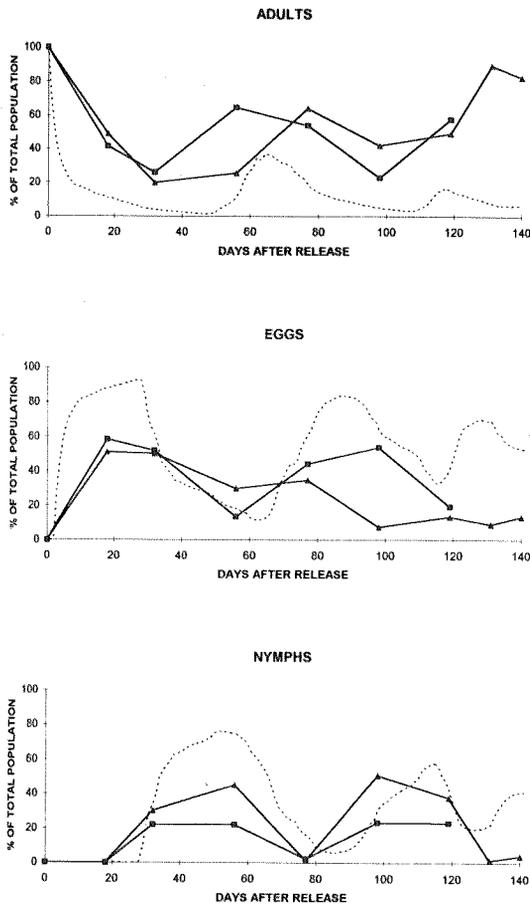


Fig. 4. Comparison of simulated (broken line) and observed phenology of marked colonies of *T. lintearius* at Fereday's Island (closed squares) and North Rakaia (closed triangles), for adults, eggs and nymphs. The timing of the peaks, not the magnitude, is relevant.

Institute of Water and Atmospheric Research) as temperature inputs (subsequently adjusted for gorse plant temperatures) and starting with overwintered females. The number of generations in each location was as follows: Lincoln (South Island) four generations and a partial fifth; Greymouth (West Coast) four generations and a partial fifth; Auckland (north of North Island) six generations. The simulations predicted that the generations would become progressively more overlapping as the season continued. During winter (assuming no diapause) the model predicted that populations in Auckland may complete another full generation, whilst in Lincoln and Greymouth they would complete only a partial generation.

Relative population growth

Survival of the overwintered females in spring was slightly higher in Lincoln and Greymouth than in Auckland, but egg production was greater in Auckland, so that by the end of spring, total population levels in Auckland were predicted to be nearly four times that in either Greymouth or Lincoln. By the end of summer, population levels in Auckland were predicted to be over 17 times those in Lincoln which were in turn predicted to be twice that in Greymouth.

Overwintering behaviour

To investigate the overwintering behaviour of the mite, simulations were started in late autumn, with a mixed population of summer females, nymphs and eggs and using climatology temperatures from Auckland, Greymouth and Lincoln. In Lincoln, the model predicted that oviposition would continue into winter, but the onset of colder temperatures caused high mortality of the females, which all died by late June. The eggs also subsequently disappeared from the population, but nymphs survived the cold temperatures, and continued to develop slowly through winter, with population levels remaining low. When the input of 'summer' females was replaced by 'winter' females, they survived until late winter, produced more eggs than 'summer' females and the population growth during winter was greater.

In the warmer winters of Auckland and Greymouth, with the same starting conditions the model predicted that 'summer' adults entering winter would die during July, but the faster population development allowed another adult generation to come through from nymphs, and all stages of the mite were present during the winter. In Greymouth the model predicted no numerical response in the mite population over winter, but in Auckland the population increased four-fold. If 'summer' adults are replaced by 'winter' adults as inputs there was little difference for Auckland but greater population growth for Greymouth during winter.

Discussion

The population model of the gorse spider mite provides excellent predictions of phenology and has enabled us to investigate many aspects of temperature-driven mite population dynamics.

As expected, the warmer North Island site of Auckland supported more mite generations than

Greymouth or Lincoln, but phenology alone is unlikely to explain differences in establishment success. At all times of the year, the model predicted a much greater capacity for population increase of *T. lintearius* in Auckland than in Lincoln, suggesting better chances of establishment in Auckland than in Lincoln. This is contrary to observations that *T. lintearius* has repeatedly failed to establish in the Auckland region, yet massive populations have occurred near Lincoln and mites are spreading rapidly. The model suggests that the temperature-driven population dynamics of mites in Auckland do not explain this failure to establish. *Tetranychus lintearius* populations in Greymouth on the other hand were predicted to reach only half the levels of populations in Lincoln by the end of summer, suggesting poorer chances of establishment. Temperatures could therefore contribute to the lack of establishment in Greymouth, with slower population growth rendering populations more susceptible to stochastic extinction (e.g. heavy rainfall).

The observation that 'overwintered' females had a different temperature response for fecundity than summer-collected females, and greater survival at low temperatures, suggests that a physiological change had occurred in mites in Lincoln during the winter. Moreover, simulations predicted that 'summer' females would not survive winters in Lincoln, whilst 'winter' females may do so. In addition, the temperature thresholds for oviposition of both 'summer' and 'winter' *T. lintearius* were exceeded during the winter in Lincoln, suggesting that it is not low temperatures that prevented winter oviposition.

Winter diapause occurs in a large number of tetranychid mites, although this has not been identified in *T. lintearius*, and Stone (1986) failed to induce diapause in adults. In Lincoln, adult females are the only mite stage found on gorse bushes during the winter, yet the model predicted that summer females would all die by early winter. If diapause is necessary for winter survival and sensitivity to photoperiod occurs within the nymphal stages (as is the case for a closely related mite, *T. urticae* Koch (Veerman 1985), the high mortality of adults and eggs during winter might serve to synchronize the population as newly-mated pre-oviposition females. If diapause can be demonstrated in *T. lintearius*, one hypothesis for establishment-difficulties might be that diapause is incomplete in Auckland and Greymouth and that heavy winter-rainfall exerts high mortality on developing

populations of eggs and nymphs.

Only a small number of simulations have been carried out so far, but the model has given considerable insight into the population dynamics of *T. lintearius* in New Zealand. It has indirectly suggested that failure to diapause could be a contributing factor to establishment-difficulties in regions with mild winters. Conditions inducing diapause should be investigated in more detail and a thorough sensitivity analysis of the model should also be carried out, with particular attention to low-temperature induced mortality which appears to be important during winter. In the future, the model will also be used to investigate the population dynamics of the new strains of mite from warmer climates.

Models have played a minor role in the understanding or management of classical biocontrol projects, because they are perceived as being too difficult to develop, or too expensive, or because their usefulness is doubted. If we are to learn from the successes and failures of biological control introductions, modelling must surely play a greater role in the future.

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