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Density dependent prey-feeding time of *Stethorus bifidus* (Coleoptera: Coccinellidae) on *Tetranychus lintearius* (Acari: Tetranychidae)

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Abstract The gorse spider mite, *Tetranychus lintearius*, a biological control agent introduced into New Zealand to control gorse, is often attacked by the endemic coccinellid, *Stethorus bifidus*. Predation by *S. bifidus* has been suggested as a reason why *T. lintearius* colonies collapse. For *S. bifidus* predation to regulate *T. lintearius* populations, at least one component of its numerical or functional response must result in an increased proportion of mites being killed as mite density increases. Laboratory experiments showed that feeding time (a sub-component of the functional response) decreased markedly with increased *T. lintearius* density. An increase in available prey density from 3–25 mites/177 mm^2 led to an exponential decrease in mean feeding time from 870 s to100 s. Furthermore, despite *S. bifidus* killing more mites, it extracted progressively smaller proportions of the contents of each mite killed as mite density increased.

Keywords *Stethorus bifidus*; beetle; *Tetranychus lintearius*; spider mite; predation; functional response; feeding time; prey density; biological control

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INTRODUCTION

The gorse spider mite *Tetranychus lintearius* (Dufour) (Acari: Tetranychidae) was introduced to New Zealand to help control gorse (*Ulex europaeus*) and is now established throughout the country (Hill et al. 1991, 1993). Damaging outbreaks of *T. lintearius* are common on *U. europaeus* but they do not persist (R. L. Hill pers. comm.).

The endemic *Stethorus bifidus* (Kapur) (Coleoptera: Coccinellidae) is found throughout New Zealand (Houston 1990) and is a specialist predator of mites. It is often found in *T. lintearius* colonies before and after they collapse. This has been suggested as one reason why *T. lintearius* colonies do not persist (R. L. Hill pers. comm.). For *S. bifidus* predation to regulate *T. lintearius* populations, either the numerical or functional response of the predator to prey density must result in an increased proportion of mites being killed per predator as prey density increases.

Houck (1991) examined handling time (a component of the functional response) in coccinellid-mite systems and found that, as the predator *Stethorus punctum* (LeConte) became starved after exposure to low mite densities, the handling time for each prey item (*Tetranychus urticae* (Koch)) increased. This was due to a greater extraction of body fluids from individual prey. Conversely, the beetles continue to feed, and were observed piercing prey, initiating feeding and subsequently abandoning prey even when satiated, resulting in shorter handling times at high densities. This demonstrates that *S. punctum* feeds on *T. urticae* in a density-dependent way.

Holling (1959) classified functional responses into three categories: type 1, where the proportion of prey killed per predator is constant as prey density increases to a threshold where the number killed per predator becomes constant; type 2, where the proportion of prey killed per predator decreases as prey density increases; and type 3, where the proportion of prey killed per predator initially increases, then decreases as prey density increases. If *S. bifidus*

is regulating *T. lintearius* through the functional response, then its functional response curve must be type 3, i.e., sigmoid; functional responses of type 1 and 2 cannot contribute to prey regulation because the proportion of prey killed per predator does not increase as prey density increases (Holling 1965). Furthermore, sigmoid functional response curves can contribute to prey regulation if average prey densities stay below a threshold prey density where the proportion of prey killed per predator is increasing with increasing prey density (Hassell 1977). A sigmoid curve will be observed only if at least one component of the functional response depends on prey density in such a way that the proportion of prey being killed per predator increases with increasing prey density.

To test the hypothesis that the functional response of *S. bifidus* results in an increased proportion of prey being killed as *T. lintearius* density increases (prey regulation), we measured feeding times (a component of handling time) of *S. bifidus* over a range of *T. lintearius* densities.

MATERIALS AND METHODS

Tetranychus lintearius were maintained at five densities in cell plates modified from the design of McMurtry et al. (1974). The plates were made by drilling 16 evenly spaced cells of 15 mm diameter into a top perspex plate (100 × 100 × 3 mm) and 16 matching ventilation holes of 8 mm diameter into a bottom perspex plate. The plates were screwed together but separated by builders' paper to prevent an airtight seal when the cells were capped with a cover slip. The plates were kept at 20.5 ± 1.5°C, 65–75% relative humidity and 16:8 L:D photoperiod. Experimental densities were 3, 5, 10, 18 and 25 *T. lintearius* per cell.

Stethorus bifidus adults were collected from apple trees at the Levin Horticultural Research Centre near Shannon and from gorse infested with *T. lintearius* on Old West Road near Palmerston North. *Tetranychus lintearius* colonies were collected from various localities, and reared in the laboratory on potted plants.

To begin each trial, *T. lintearius* were counted into cells and one *S. bifidus* female added to each of 15 cells at each density. Every 12 h for 72 h thereafter, the experiment was reset by moving each of the *S. bifidus* to a new cell stocked with the initial number of *T. lintearius*. This gave *S. bifidus* time to attain hunger levels that reflected each prey density. After 72 h we again moved each of the *S. bifidus* to a new cell, but this time recorded the time it took to eat their first mite. We re-fed the same beetles and re-measured their feeding time again after a further 12 h.

We defined feeding time as beginning only after the predator had secured the prey and started feeding. If *S. bifidus* released a *T. lintearius* momentarily we stopped timing, and then re-started after it had been re-secured. Each *S. bifidus* was tested at each mite density.

We also estimated the amount of body contents extracted from each captured *T. lintearius* by giving the cadavers a visual score of either 1, 2 or 3. We called this the index of extraction, and calculated a mean index of extraction for each density.

RESULTS

Feeding time decreased exponentially as prey density increased (Fig. 1). When prey density was 3 per cell, *S. bifidus* fed on each *T. lintearius* for up to 10 times longer than when *T. lintearius* density was 25 per cell.

Extraction indices support feeding time data. As feeding time increased, more body contents were removed (Fig. 2).

DISCUSSION

Our results support Houck's (1991) finding, that the feeding behaviour of a predatory coccinellid depends on prey density. At high prey densities, the predator spends less time feeding on each prey individual before searching for another. Therefore, below a given density, we would expect this predator to kill a higher proportion of prey from a dense population than from a sparse population.

There are two explanations for the shorter feeding time at high prey densities: either the predator is being disturbed while feeding, increasing the probability that it will move and resume searching; or the predator finds it progressively harder to extract food from a prey individual, thus making it more attractive to catch another prey. The latter explanation requires the predator to recognise prey density. Both explanations may be true.

Handling time is the time required for a predator to pursue, subdue, eat and digest the prey (Holling 1965). Given that Houck (1991) concluded that the handling time for each prey item (*Tetranychus*

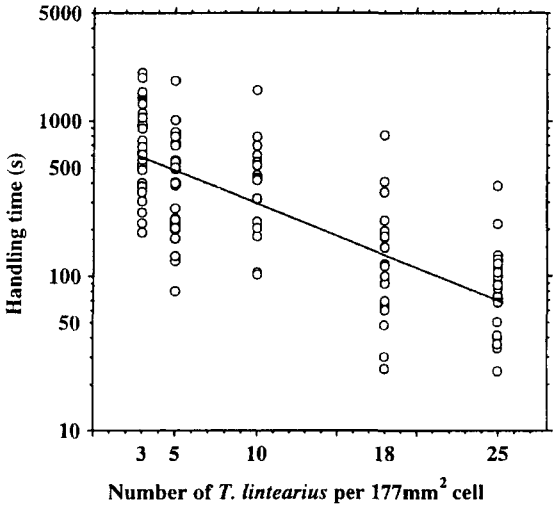

Fig. 1 Handling time for *S. bifidus* preying on *T. lintearius*. Regression equation is: Log_{10}(Handling time) = 2.894–0.042 (*T. lintearius* density). R2 = 0.56. $P < 0.01$.

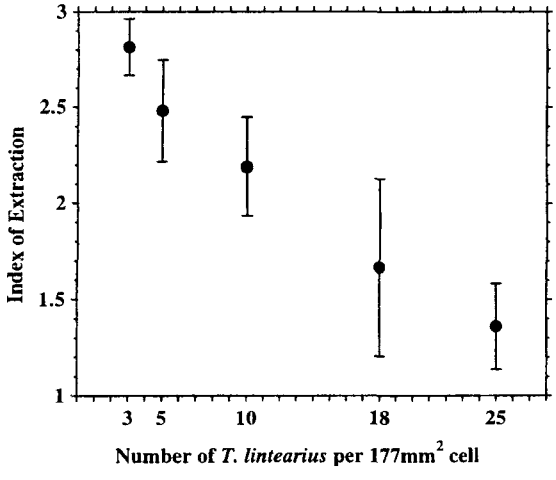

Fig. 2 Mean extraction indices measured at each *T. lintearius* density; ± 1.96 × standard error of mean. 1 = very slight feeding or a 'stab', 2 = approximately half of the mite body contents were removed leaving the mite dead, and 3 = extensive extraction of body contents leaving only a chalky-appearing mite exoskeleton.

urticae (Koch)) increased as body fluids were extracted more completely from individual prey, we suggest that our measurements of *S. bifidus* feeding time on *T. lintearius* were strongly correlated to actual handling times.

Therefore, our results suggest that *S. bifidus* has a sigmoid functional response to *T. lintearius* density, because the handling time (a component of the functional response) decreases, allowing an increasing proportion of prey to be killed, as prey density increases. This supports the hypothesis that *S. bifidus* has the potential to regulate *T. lintearius*.

Given that *T. lintearius* was introduced to control gorse but is itself vulnerable to control by an endemic predator, suggests that its effectiveness as a biocontrol agent may be limited.

However, simple laboratory arenas clearly differ from field conditions, and we do not know how prey density in these artificial trials relates to prey density in field populations. Our cells were a simple habitat, and we know that *T. lintearius* live in highly complex habitats of gorse enveloped in silk webbing. The predator's perception of prey density in that complex habitat presumably differs from that in the laboratory. Therefore, an obvious direction for future work would be to relate handling times measured in this artificial laboratory situation to those measured in more complex habitats, particularly those that more closely approximate the natural environment of *T. lintearius*.

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