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The effect of prey species and environmental complexity on the functional response of *Franklinothrips orizabensis*: a test of the fractal foraging model

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Abstract. 1. The hypothesis proposed by the fractal foraging model, that prey procurement by predators declines as habitat complexity increases, was tested. To evaluate this hypothesis, the effect of two prey species, second-instar larvae of *Scirtothrips perseae* Nakahara and *Heliothrips haemorrhoidalis* (Bouché) (both Thysanoptera: Thripidae), and environmental complexity on the functional response of the predatory thrips *Franklinothrips orizabensis* Johansen (Thysanoptera: Aeolothripidae) was examined.

2. The Koch curve, a well-studied fractal, was used to generate the shapes of experimental arenas to test the effect of environmental complexity on the functional response of *F. orizabensis*. Complexity was defined in terms of the number of acute vertices in which prey thrips could seek refuge and the length of the perimeter that had to be searched by the predator. Four shapes were tested: a circle (zero acute vertices, circumference = 186.61 mm), equilateral triangle (three acute vertices, perimeter = 240 mm), star (six acute vertices, perimeter = 277.13 mm), and snowflake (18 acute vertices, perimeter = 333.65 mm). All shapes were scaled so that the area of each arena was 2771 mm^2.

3. *Franklinothrips orizabensis* exhibited a Type II functional response for both prey species and all four experimental arenas tested. Significantly fewer *S. perseae* larvae were killed in the most complex arena (i.e. the snowflake) when prey densities exceeded 16. For *H. haemorrhoidalis*, significant differences in mortality were observed only when prey densities equalled four. These results demonstrated that the fractal foraging model was supported when certain prey densities coincided with particular levels of environmental complexity.

4. Subtle changes in environmental complexity and different prey species of varying density can affect prey–predator interactions significantly.

Key words. Fractal, functional response, *Heliothrips haemorrhoidalis*, Koch curve, *Scirtothrips perseae*, spatial heterogeneity.

Introduction

Natural enemies forage in complex environments and can encounter a diversity of prey species that are distributed patchily on a variety of host plants. Subsequent interactions and attack rates by natural enemies on discovered prey can be affected by several factors including the chemical and physical properties of the host plant (Messina & Hanks, 1998; Cloyd & Sadof, 2000; De Clercq *et al.*, 2000), the sex of the natural enemy and species of prey being attacked (Parajulee *et al.*, 1994; Donnelly & Phillips, 2001), spatial distribution of prey (Ryoo, 1996), searching capacity and subsequent arrestment at host patches (Ives *et al.*, 1993; Neuenschwander & Ajuonu, 1995; Hoddle *et al.*, 1998), and the presence of alternative prey (Chesson, 1989). Consequently, this complexity can affect the ability of upper trophic level organisms to search effectively for and detect resources and ultimately to regulate pest populations.

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It has been suggested that resource distributions and the habitats within which they are located are fractal in nature (Ritchie, 1998), i.e. perimeters, surface areas, or densities increase as the scale used by the forager to measure them decreases (Gleick, 1987; Smith, 1998). Fractal environments affect resource consumption because the geometry of the environment perceived by the consumer is scale-dependent (e.g. potential host habitat viewed as a clump of plants, a single plant, then as a branch, and ultimately as a leaf or fruit and its associated surface topography). This hierarchy affects detection and processing of suitable resources within that habitat. Therefore, a consumer's encounter rates with resource patches depend on the fractal dimensions of the habitat being searched and the spatial distribution and density of prey in the environment. For example, in studies that limited exposure times of natural enemies to prey, attack rates were reduced as plant height, leaf number, leaf surface area, and branch number increased (Cloyd & Sadof, 2000). Consequently, the fractal foraging model links resource consumption rates to the geometry of foraging landscapes and predicts that as habitat structure becomes more structurally complex, the foraging success and consumption rates of consumers will subsequently decline as resource procurement becomes more difficult (Ritchie, 1998).

Phytophagous thrips are typically small insects that are extremely thigmotactic and feed, pupate, and oviposit preferentially in protected areas on host plants, especially along leaf veins, under calyces, or among clusters of touching fruit (Lewis, 1973). Two serious thrips pests of avocados *Persea americana* Miller in southern California, U.S.A., that exhibit strong thigmotactic behaviour are *Scirtothrips perseae* Nakahara (Hoddle, 2002) and *Heliothrips haemorrhoidalis* (Bouché) (McMurtry *et al.*, 1991) (both Thysanoptera; Thripidae). *Franklinothrips orizabensis* Johansen (Thysanoptera: Aeolothripidae) is a generalist predator thrips, found in California avocado orchards, that readily attacks *S. perseae* and *H. haemorrhoidalis* larvae (Hoddle *et al.*, 2001a). Because of their small size and thigmotactic behaviour, *S. perseae* and *H. haemorrhoidalis* are ideal candidates with which to evaluate the effect of fractal environments on the ability of a generalist predator to find and consume them.

The prediction of the fractal foraging model, that prey procurement declines as habitat complexity increases, was evaluated in this study by determining the functional response of *F. orizabensis* when exposed to different densities of either *S. perseae* or *H. haemorrhoidalis* larvae in arenas of differing complexity. The functional response is simply the number of prey attacked by a predator as a function of prey density (Solomon, 1949) and has figured prominently in foraging theory and population modelling (Juliano, 1993). The functional response type (I, II, or III) is characterised by the shape of the curve that describes attack rates over increasing prey densities by predators within a fixed exposure period (Juliano, 1993). In this study, arena complexity, or spatial heterogeneity, was derived from a well-studied fractal, the Koch curve (Gleick, 1987; Smith,

1998), and the number of acute vertices available for thrips to hide in while feeding and the perimeter length to be searched by *F. orizabensis* were used to define environmental complexity. The area of each experimental arena was held constant as complexity increased, thereby avoiding confounding increasing complexity with increasing area to be searched by predators.

Materials and methods

Sources of prey thrips and predators

Scirtothrips perseae larvae were collected from a heavily infested 'Hass' avocado orchard in Bonsall, California. Immature avocado leaves with thrips were removed from the orchard, placed in plastic bags, and returned to the laboratory in a cooler. Second-instar larvae were removed from leaves with the aid of a dissecting microscope and fine paintbrush, and placed at pre-determined densities in one of the four experimental arenas (see below). A *H. haemorrhoidalis* colony was maintained at 25–27 °C under L:D 14:10 h photoperiod on green lemons at the University of California at Riverside. Second-instar larvae were removed from lemons with the aid of a dissecting microscope and fine paintbrush, and placed at pre-determined densities in one of the four experimental arenas (see below). *Franklinothrips orizabensis* was reared at the University of California following methods outlined by Hoddle *et al.* (2000) and this colony was the source of predators used for experiments. Predators were harvested from cages as pupae in parafilm cones (Hoddle *et al.*, 2001b) and held individually in glass vials until adults emerged. Unmated and unfed adult female *F. orizabensis* ≈24 h old were used in all functional response experiments.

Experimental arenas

Modified Munger cells constructed from clear acrylic plastic (Morse *et al.*, 1986) were used as experimental arenas that enclosed thrips prey with *F. orizabensis*. The middle section of the Munger cell was cut to provide one of the four experimental shapes used to test environmental complexity on predator searching efficacy. The number of acute vertices in which thrips larvae could seek refuge from predators and the length of the shape's perimeter classified the environmental complexity of each shape. The four shapes tested in order of increasing environmental complexity were: (1) circle (zero acute vertices, circumference = 186.61 mm, radius = 29.70 mm), (2) equilateral triangle (three acute vertices, perimeter = 240 mm, length of side = 80 mm), (3) star (six acute vertices, perimeter = 277.13 mm), and (4) snowflake (18 acute vertices, perimeter = 333.65 mm) (Fig. 1).

The star and snowflake are Koch curves. To generate the star shape, the equilateral triangle had a new triangle one-third the size added to the middle of each side. This was
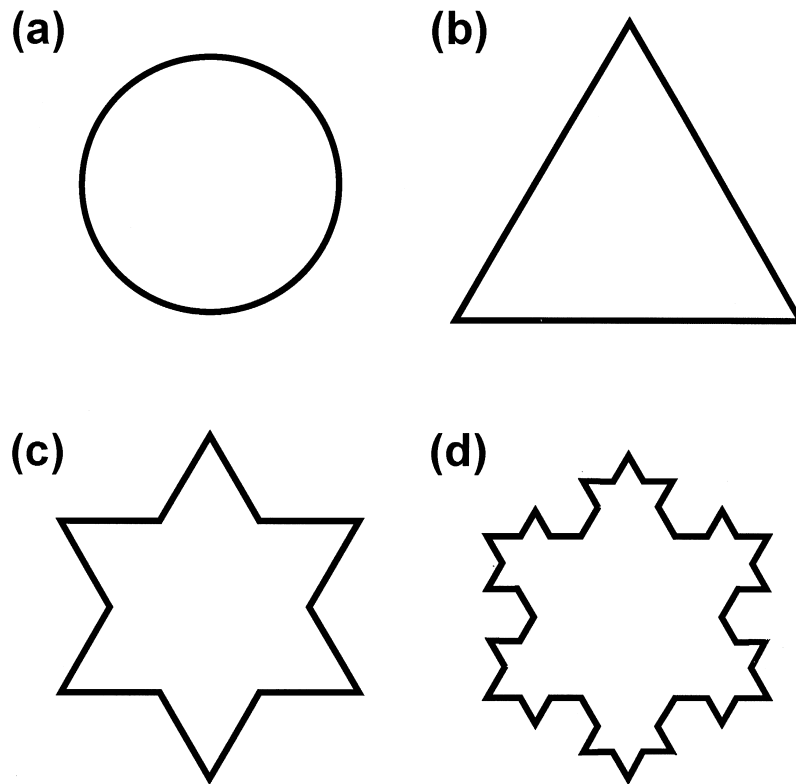
Fig. 1. Experimental arenas used to test the effect of increasing environmental complexity on the functional response of *Franklinothrips orizabensis* attacking *Scirtothrips perseae* and *Heliothrips haemorrhoidalis*. (a) Circular, (b) triangular, (c) star-, and (d) snowflake-shaped arenas. All shapes were scaled so that the area to be searched by *F. orizabensis* was 2771 mm^2.

repeated for the star shape and the snowflake shape was derived (Gleick, 1987; Smith, 1998). All experimental shapes were scaled to ensure that the area to be searched by *F. orizabensis* was 2771 mm^2, thus preventing confounding the increasing area to be searched with increasing complexity. The middle section of the Munger cell with the shape being tested was used to enclose an immature three-quarters-expanded 'Hass' avocado leaf placed on water-saturated blotting paper. The avocado leaf provided the foraging substrate for prey and predators.

Experimental set-up

Thrips larvae were placed in Munger cells and allowed to acclimate and select feeding and hiding places 24 h before predators were introduced into arenas. *Scirtothrips perseae* larvae are relatively mobile and dispersed readily from the central placement within Munger cells to the perimeters and vertices of arenas. *Heliothrips haemorrhoidalis* larvae, on the other hand, are relatively immobile and to ensure distribution within arenas, larvae were placed individually according to randomly generated *x*–*y* coordinates selected from a grid that overlaid the clear acrylic top panel of the Munger cell. Thrips larvae were placed into each experimental arena at a rate of one, two, four, eight, and

16 larvae. *Scirtothrips perseae* was presented to *F. orizabensis* at one additional density of 25 larvae. *Franklinothrips orizabensis* females were introduced into Munger cells and allowed to forage for 24 h. At the end of the foraging period, predators were removed, and numbers of live and dead thrips larvae were recorded. Each Munger cell that contained thrips larvae and predators was paired with a control cell (same experimental shape and thrips density) that did not contain a predator. These control cells provided an estimate of naturally occurring mortality of thrips larvae due to causes other than predation. All paired Munger cells were kept in a temperature controlled cabinet at 25 °C under long days (LD 14:10 h) for the 24-h foraging period.

Statistical analyses

Predator functional response data for each experimental shape and prey species were analysed in two stages. (1) The shape of the functional response curve was determined by logistic regression of the proportion of thrips prey eaten as a function of initial density (Trexler *et al.*, 1988; Trexler & Travis, 1993). (2) The *random predator* equation was fitted to data after the functional response type was determined (Juliano, 1993).

The polynomial function from Juliano (1993):

$$\frac{N_e}{N_0} = \frac{exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}{1 + exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)} \quad (1)$$

where N_e is the number of thrips eaten, N_0 is the initial prey density, and N_e/N_0 is the probability of being eaten, was fitted to data on the proportion of thrips killed. Maximum likelihood estimates of parameters P_0 to P_3 were obtained by applying logistic regression (Proc Logistic) in SAS (SAS, 1990) to a dichotomous variable that equalled 0 for surviving thrips and 1 for consumed thrips. From this approach, one criterion for separating Type I to III functional responses is to analyse the proportion of prey eaten and test for significant positive or negative linear coefficients from eqn 1. Consequently, the signs of the linear, quadratic, and cubic coefficients from eqn 1 can be used to distinguish the shape of the functional response from experimental data (Juliano, 1993). Linear terms not significantly different from 0 indicate a Type I functional response, a significant negative linear coefficient indicates a Type II response, while a significant positive linear term indicates a Type III response (Juliano, 1993). To determine the significance of the linear term from eqn 1, the log likelihood-ratio test was used to determine whether equation coefficients differed significantly from 0 (Trexler & Travis, 1993). In this test, the difference in log-likelihoods is a chi-square value (χ^2) with 1 d.f.

Once the functional response type was determined from logistic regression analyses and log likelihood-ratio tests, iterative non-linear least squares regression (SAS, 1990) was used to fit the *random predator* equation to data. This equation accounts for prey depletion without replenishment in functional response assays to data (Rogers, 1972):

$$N_e = N_0\{1 - exp[a(T_h N_e - T)]\} \quad (2)$$

where N_e = number of thrips eaten, N_0 = initial density of prey, a = attack constant, T_h = handling time, and T = total time available for attack (24 h). The random predator equation was fitted to plots of raw data of number of thrips prey killed at each prey density tested to improve standard error estimates of a and T_h (Juliano & Williams, 1987; Williams & Juliano, 1996). Model parameter estimates (a and T_h) were then compared within prey species and across shapes with Proc NLIN in SAS (SAS, 1990) and separation of statistically different parameter estimates was made using 95% confidence intervals in SAS (SAS, 1990). Parameter estimates were not significantly different if comparisons produced 95% confidence intervals that included zero (Juliano, 1993).

Analysis of covariance with control mortality as the covariate was performed in SAS (SAS, 1990) to determine whether significant prey mortality occurred due to causes other than exposure to predators. Analysis of covariance did not indicate a significant contribution to mortality rates due to natural causes (see results). Mean number of prey attacked by species and density was compared across shapes using a two-way ANOVA. Detection of a significant

interaction term (shape $\times$ density) was detected for both prey species (see results) and one-way ANOVA was used to determine whether the mean number of larvae consumed at the density tested differed significantly across shapes for each prey species. Separation of statistically different means was made using Tukey's Studentised Range Test in SAS at the 0.05 level of significance (SAS, 1990).

Results

Determination of functional response type

Scirtothrips perseae as prey. For all experimental shapes tested, *F. orizabensis* exhibited a Type II functional response because the linear term of eqn 1 was both negative and significantly different from 0, indicating that the proportion of prey killed declined significantly as prey density increased (Table 1). Quadratic terms were not derived for the circular and triangular shapes, indicating that in these arenas and at the prey densities tested, prey saturation of *F. orizabensis* did not occur because the asymptotic plateau of proportion of prey killed was not reached (Table 1). A significant negative linear coefficient and a non-significant quadratic term are compatible with a Type II response (Trexler *et al.*, 1988). A quadratic term for the star shape was derived but did not differ significantly from 0, indicating the same result as that for the circular and triangular arenas (Table 1). A significant quadratic term was derived for the snowflake arena, indicating that an asymptotically declining proportion of prey killed by *F. orizabensis* was achieved with this shape (Table 1).

Heliothrips haemorrhoidalis as prey. For all experimental shapes tested, *F. orizabensis* exhibited a Type II functional response, indicated by negative linear terms that differed significantly from 0 and quadratic terms that were significant, indicating that an asymptotically declining proportion of prey killed had resulted (Table 2).

Table 1. Maximum likelihood estimates from logistic regression of the proportion of *Scirtothrips perseae* eaten by *Franklinothrips orizabensis* as a function of initial prey density.

Arena shape	Parameter	Estimate ($\pm$SE)	d.f.	χ^2 value	P
Circle	Intercept	3.299 ± 0.400	1	68.01	<0.005
	Linear	-0.082 ± 0.019	1	19.39	<0.005
	Quadratic	–	–	–	–
Triangle	Intercept	3.009 ± 0.330	1	83.13	<0.005
	Linear	-0.106 ± 0.015	1	47.39	<0.005
	Quadratic	–	–	–	–
Star	Intercept	3.837 ± 0.698	1	30.19	<0.005
	Linear	-0.259 ± 0.087	1	8.81	<0.005
	Quadratic	0.005 ± 0.003	1	3.58	>0.05
Snowflake	Intercept	3.925 ± 0.082	1	36.70	<0.005
	Linear	-0.339 ± 0.082	1	17.15	<0.005
	Quadratic	0.008 ± 0.002	1	10.45	<0.005

Table 2. Maximum likelihood estimates from logistic regression of the proportion of *Heliothrips haemorrhoidalis* eaten by *Franklinothrips orizabensis* as a function of initial prey density.

Arena shape	Parameter	Estimate ($\pm$ SE)	d.f.	χ^2 value	P
Circle	Intercept	4.159 ± 0.785	1	28.09	<0.005
	Linear	-0.942 ± 0.184	1	26.07	<0.005
	Quadratic	0.036 ± 0.009	1	16.09	<0.005
Triangle	Intercept	5.707 ± 1.586	1	12.96	<0.005
	Linear	-2.887 ± 0.826	1	12.23	<0.005
	Quadratic	0.372 ± 0.115	1	10.51	<0.005
	Cubic	-0.014 ± 0.004	1	10.32	<0.005
Star	Intercept	4.588 ± 1.347	1	11.61	<0.005
	Linear	-2.513 ± 0.745	1	11.38	<0.005
	Quadratic	0.320 ± 0.107	1	9.06	<0.005
	Cubic	-0.012 ± 0.004	1	8.27	<0.005
Snowflake	Intercept	3.711 ± 1.217	1	9.30	<0.005
	Linear	-2.077 ± 0.686	1	9.16	<0.005
	Quadratic	0.262 ± 0.099	1	7.01	0.008
	Cubic	-0.010 ± 0.004	1	6.32	0.012

Functional response parameter estimates

Scirtothrips perseae *as prey*. The fit of the *random predator* equation to number of *S. perseae* larvae killed as a function of density was significant for the circular (ANOVA: $F_{2,58} = 947$, $P < 0.005$) (Fig. 2a), triangular (ANOVA: $F_{2,58} = 415$, $P < 0.005$) (Fig. 2b), star-shaped (ANOVA: $F_{2,58} = 316$, $P < 0.005$) (Fig. 2c), and snowflake-shaped (ANOVA: $F_{2,58} = 577$, $P < 0.005$) (Fig. 2d) arenas. No significant differences in attack constant (*a*) estimates for *F. orizabensis* were observed across shapes (Table 3). The handling time (T_h) parameter estimate for *F. orizabensis* attacking *S. perseae* larvae in the triangular arena was significantly greater than in the circular arena but similar to handling time estimates for the star- and snowflake-shaped arenas (Table 3).

Heliothrips haemorrhoidalis *as prey*. The fit of the *random predator* equation to the number of *H. haemorrhoidalis* larvae killed as a function of density was significant for the circular (ANOVA: $F_{2,48} = 102$, $P < 0.005$) (Fig. 3a), triangular (ANOVA: $F_{2,48} = 59$, $P < 0.005$) (Fig. 3b), star-shaped (ANOVA: $F_{2,48} = 72$, $P < 0.005$) (Fig. 3c), and snowflake-shaped (ANOVA: $F_{2,48} = 71$, $P < 0.005$) (Fig. 3d) arenas. Significant differences in attack constant (*a*) estimates for *F. orizabensis* were observed, with attack constant estimates being substantially lower for the star- and snowflake-shaped arenas (Table 4). The handling time (T_h) parameter estimate was significantly higher for *F. orizabensis* attacking *H. haemorrhoidalis* in triangular arenas (Table 4).

Effect of arena shape on prey consumption rates

Scirtothrips perseae *as prey*. Analysis of naturally occurring mortality for *S. perseae* larvae not exposed to

F. orizabensis in experimental arenas using ANCOVA showed that it was not a significant cause of death (just 0–6% of control larvae died in a 24-h period) for any of the experimental prey densities and arenas tested. Consequently, naturally occurring mortality of prey exposed to predators was negligible and thrips death was assumed to have resulted entirely from predation. The interaction term (shape × density) from the two-way ANOVA was significant (ANOVA: $F_{15} = 2.98$, $P < 0.001$), indicating significant differences in mortality as a result of the shape of the experimental arena. A density of one *S. perseae* larvae resulted in 100% predation mortality across all experimental arenas (Table 5). No significant differences in mortality rates across experimental arenas were observed for densities of two (ANOVA: $F_{3,36} = 0.75$, $P = $NS), four (ANOVA: $F_{3,36} = 1.48$, $P = $NS), or eight (ANOVA: $F_{3,36} = 1.09$, $P = $NS) *S. perseae* larvae. Significant differences in mortality rates were observed at densities of 16 (ANOVA: $F_{3,36} = 4.25$, $P < 0.05$) and 25 (ANOVA: $F_{3,36} = 3.55$, $P < 0.05$) thrips larvae, with fewer *S. perseae* being found and killed in more complex environments (Table 5).

Heliothrips haemorrhoidalis *as prey*. Analysis of naturally occurring mortality for *H. haemorrhoidalis* larvae not exposed to *F. orizabensis* in experimental arenas using ANCOVA showed that it was not a significant cause of death (just 0–4% of control larvae died in a 24-h period) for any of the experimental prey densities and arenas tested. Consequently, naturally occurring mortality of prey exposed to predators was negligible and thrips death within experimental arenas was assumed to have resulted entirely from predation. The interaction term (shape × density) from the two-way ANOVA was significant (ANOVA: $F_{15} = 2.32$, $P < 0.05$), indicating significant differences in mortality as a result of the shape of the experimental arena. No significant differences in mortality rates across experimental arenas were observed for densities of one (ANOVA: $F_{3,36} = 1.00$, $P = $NS), two (ANOVA: $F_{3,36} = 2.71$, $P = $NS), eight (ANOVA: $F_{3,36} = 0.36$, $P = $NS), or 16 (ANOVA: $F_{3,36} = 2.38$, $P = $NS) *H. haemorrhoidalis* larvae per arena. A significant difference in mean number of *H. haemorrhoidalis* larvae killed occurred at a density of four larval thrips per experimental arena (ANOVA: $F_{3,36} = 5.11$, $P < 0.01$) (Table 6). At this larval density, significantly fewer *H. haemorrhoidalis* larvae were found and killed in triangular, star-, and snowflake-shaped arenas than in the circular arena (Table 6).

Discussion

Increasing environmental complexity and prey species had significant effects on the functional response of *F. orizabensis*. A Type II functional response (i.e. the mean number of prey killed hyperbolically approached an asymptote while the proportion of prey killed declined asymptotically, indicating negative density-dependent mortality; Juliano, 1993) for both prey species across all experimental arenas.
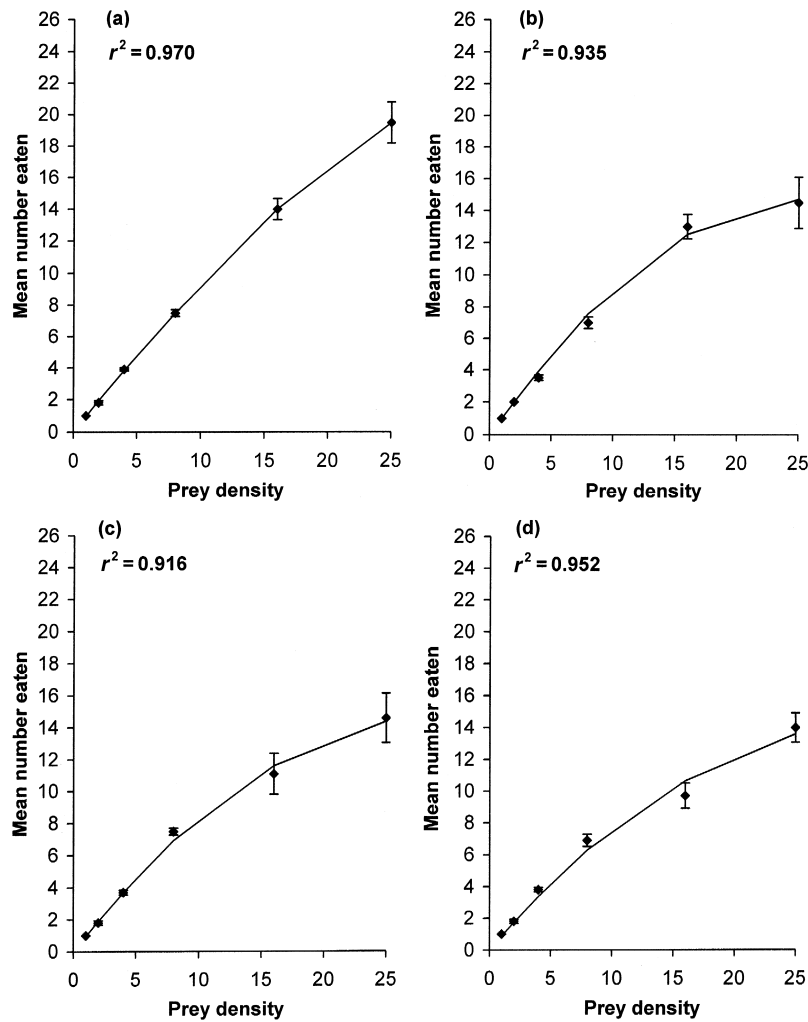
Fig. 2. Functional response curves for *Franklinothrips orizabensis* foraging for *Scirtothrips perseae* in (a) circular, (b) triangular, (c) star-, and (d) snowflake-shaped arenas. Observed experimental values ($\pm$ SE) are shown as symbols to which the random predator equation was fitted (lines).

When *S. perseae* was presented as prey, the Type II functional response was most pronounced in the most complex environment (i.e. the snowflake), indicated by a significant quadratic term from logistic regression analysis. Handling times (T_h) were higher for arenas that had vertices (in particular the triangle) that needed to be searched, but

estimates of attack rates (a) were not significantly different across arenas. Significantly more *S. perseae* were killed in the least complex arena (circle) and significantly fewer thrips were killed in the most complex arena (snowflake) when prey densities exceeded 16 larvae. When fewer than 16 *S. perseae* larvae were presented, no significant

Table 3. Mean ($\pm$ SE) estimates of the attack constant [a (h^{-1})] and handling time [T_h(h)] for *Franklinothrips orizabensis* females attacking second-instar *Scirtothrips perseae* larvae in arenas of varying complexity. Means followed by the same letters within rows are not significantly different (comparison of 95% confidence intervals).

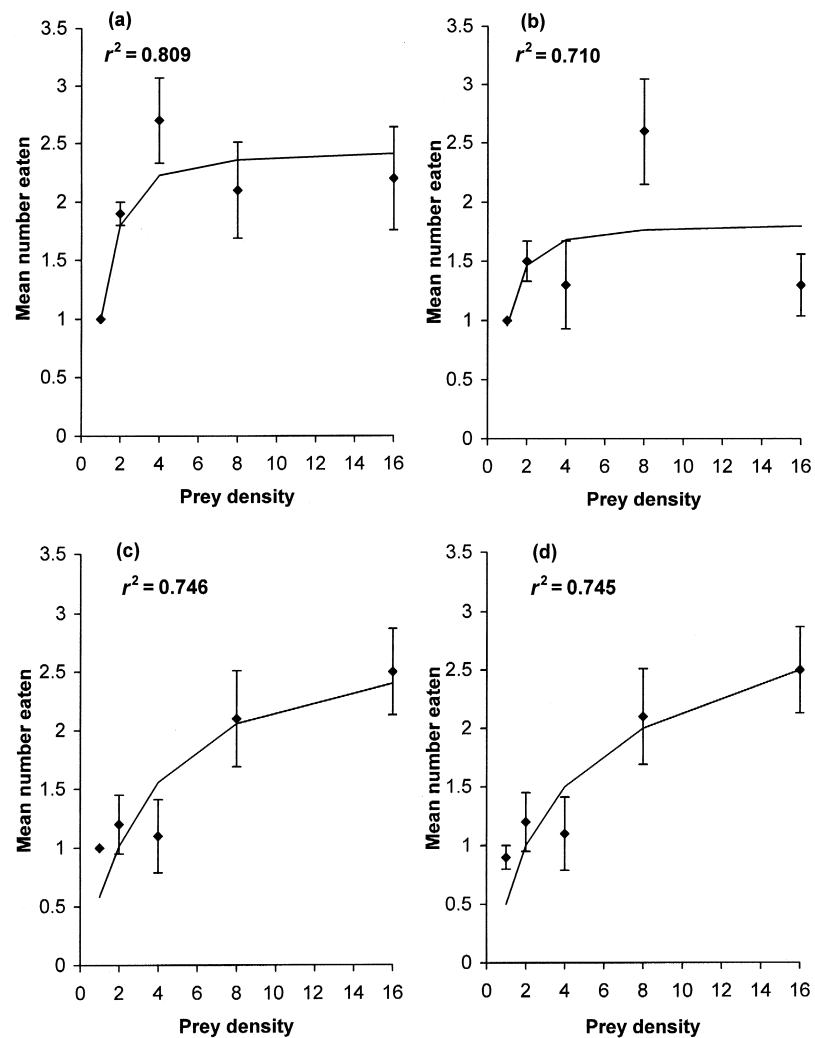| Parameter	Shape of experimental arena			
	Circle	Triangle	Star	Snowflake
a	0.15 ± 0.04a	0.21 ± 0.12a	0.13 ± 0.05a	0.09 ± 0.02a
T_h	0.70 ± 0.18a	1.34 ± 0.21b	1.21 ± 0.24ab	1.13 ± 0.19ab

Fig. 3. Functional response curves for *Franklinothrips orizabensis* foraging for *Heliothrips haemorrhoidalis* in (a) circular, (b) triangular, (c) star-, and (d) snowflake-shaped arenas. Observed experimental values ($\pm$ SE) are shown as symbols to which the random predator equation was fitted (lines).

differences in mean numbers of prey killed were observed, indicating that at these densities and an exposure time of 24 h, *F. orizabensis* was able to locate and kill similar numbers of prey irrespective of the number of vertices in which larvae were able to hide.

Attack rates (a) of *F. orizabensis* were reduced significantly by $\approx$80–86% in star- and snowflake-shaped arenas when *H. haemorrhoidalis* was presented as prey, but handling times (T_h) were only significantly higher in the triangular arena. This was also observed when *S. perseae*

Table 4. Mean ($\pm$ SE) estimates of the attack constant [a (h^{-1})] and handling time [T_h(h)] for *Franklinothrips orizabensis* females attacking late second-instar *Heliothrips haemorrhoidalis* larvae in arenas of varying complexity. Means followed by the same letters within rows are not significantly different (comparison of 95% confidence intervals).

	Shape of experimental arena			
Parameter	Circle	Triangle	Star	Snowflake
a	0.36 ± 0.04a	0.27 ± 0.10a	0.05 ± 0.02b	0.04 ± 0.02b
T_h	9.77 ± 0.75a	13.09 ± 1.36b	8.52 ± 1.74a	8.33 ± 1.73a

Table 5. Mean number ($\pm$ SE) of *Scirtothrips perseae* larvae killed by female *Franklinothrips orizabensis* in experimental arenas. Means followed by the same letters within rows are not significantly different (ANOVA, $P > 0.05$).

Density of *S. perseae* larvae	Shape of experimental arena			
	Circle	Triangle	Star	Snowflake
1	$1.00 \pm 0.00a$	$1.00 \pm 0.00a$	$1.00 \pm 0.00a$	$1.00 \pm 0.00a$
2	$1.80 \pm 0.13a$	$2.00 \pm 0.00a$	$1.80 \pm 0.13a$	$1.80 \pm 0.13a$
4	$3.90 \pm 0.10a$	$3.50 \pm 0.17a$	$3.70 \pm 0.15a$	$3.80 \pm 0.13a$
8	$7.50 \pm 0.22a$	$7.00 \pm 0.37a$	$7.50 \pm 0.22a$	$6.90 \pm 0.38a$
16	$14.00 \pm 0.67a$	$13.00 \pm 0.77a$	$11.10 \pm 1.29ab$	$9.70 \pm 0.80b$
25	$19.50 \pm 1.30a$	$14.50 \pm 1.61ab$	$14.60 \pm 1.54ab$	$14.00 \pm 0.92b$

was presented for attack in this shape. This result in the triangular arena for both prey species may have been observed because groups of prey were clustered in the three vertices, reducing the ability of a predator to isolate and attack individual larvae successfully. This effect could have become more pronounced at higher prey densities as predator access to individual thrips larvae would become more difficult due to more larvae being clustered together.

Significantly fewer *H. haemorrhoidalis* larvae were killed in the triangular, star-, and snowflake-shaped arenas at densities of four prey per arena. At prey densities higher and lower than four larvae, there were no significant differences in the mean number of larvae killed. This suggests that under the time and environmental complexity constraints, *F. orizabensis* was able to locate and kill similar numbers of prey at low densities (<4), and at higher prey densities (>4) prey were easier to locate because they were more abundant and satiation occurred once approximately two larvae were consumed, thereby diminishing the effect of environmental complexity on attack rates.

At prey densities exceeding four, *F. orizabensis* consistently killed greater numbers of *S. perseae* than *H. haemorrhoidalis* in all experimental arenas. There are two reasons for this: second-instar *S. perseae* larvae are substantially smaller than *H. haemorrhoidalis*, and they lack protective faecal droplets carried on the tip of the abdomen that are used to deter predator attack. Therefore, larger prey size probably satiated *F. orizabensis* more rapidly, leading to attack on fewer *H. haemorrhoidalis* larvae, and prey processing times were greater because of increased consumption times and the need to circumvent

defensive faecal droplets. Consequently, averaged T_h estimates across all experimental arenas for *F. orizabensis* attacking *H. haemorrhoidalis* were approximately nine times higher than estimates for *S. perseae*.

The results of this study support, in part, the prediction from the fractal foraging model (Ritchie, 1998) that increasing environmental complexity (defined in this study by the number of acute vertices available for prey to hide in and the perimeter length to be searched) had an adverse influence on predator foraging success. For *F. orizabensis*, the number of prey attacked and killed declined as environmental complexity increased because refugia in the form of acute vertices were more abundant and the perimeter of the arena to be searched was greater (the perimeter of the snowflake was 79% longer than the circle); the impact of the environment on predator efficacy was influenced significantly by the species of prey being attacked and the density of prey in a given habitat type, both of which had a significant influence on predator attack rates, handling times, and mean numbers of prey killed. Similar results have been found for predators searching for prey on whole plants, where leaf morphology (Evans, 1976; Kareiva & Sahakian, 1990; Messina & Hanks, 1998), leaf overlap (Kareiva & Perry, 1989), trichomes (De Clercq *et al.*, 2000), and habitat spatial structure (Kaiser, 1983) reduced predator efficacy in comparison with similar but less structurally complex foraging substrates because searching behaviours were altered and predators became less efficient at locating prey (Kareiva, 1987; Kareiva & Perry, 1989).

Increasing environmental complexity can influence attack rates of upper trophic level organisms significantly and

Table 6. Mean number ($\pm$ SE) of *Heliothrips haemorrhoidalis* larvae killed by female *Franklinothrips orizabensis* in experimental arenas. Means followed by the same letters within rows are not significantly different (ANOVA, $P > 0.05$).

Density of *H. haemorrhoidalis* larvae	Shape of experimental arena			
	Circle	Triangle	Star	Snowflake
1	$1.00 \pm 0.00a$	$1.00 \pm 0.00a$	$1.00 \pm 0.00a$	$0.90 \pm 0.00a$
2	$1.90 \pm 0.10a$	$1.50 \pm 0.17a$	$1.20 \pm 0.25a$	$1.20 \pm 0.25a$
4	$2.70 \pm 0.37a$	$1.30 \pm 0.37b$	$1.10 \pm 0.31b$	$1.10 \pm 0.31b$
8	$2.10 \pm 0.41a$	$2.60 \pm 0.45a$	$2.10 \pm 0.41a$	$2.10 \pm 0.41a$
16	$2.20 \pm 0.44a$	$1.30 \pm 0.26a$	$2.50 \pm 0.37a$	$2.50 \pm 0.37a$

provide refuges from attack, thus reducing the efficacy of biological control (Hawkins *et al*., 1993). In some situations, increased environmental complexity in the form of leaf domatia (i.e. tufts of hair or other minute structures in leaf vein axils) almost exclusively enhances predator densities (e.g. phytoseiid mites) in comparison with leaves that lack domatia (Walter & O'Dowd, 1992; Walter, 1996). Increased predator densities because of domatia generally result in enhanced biological control of phytophagous pests and improved plant reproductive performance (Agrawal & Karban, 1997; Agrawal *et al*., 2000) but natural enemies may not suppress herbivore densities consistently (Agrawal, 1997). Domatia increase the complexity of the phylloplane and appear to protect natural enemies from intra-guild predation (Norton *et al*., 2001), and may reduce abiotic stress (e.g. low humidity) experienced by small predators (Walter & O'Dowd, 1992) that together can increase natural enemy efficacy.

Consequently, the structure of the environment to be searched, the pest and natural enemy distribution and behaviour within that environment collectively challenge the foraging efficacy of biological control agents and are components of a dynamic and interactive system that require thorough understanding if the mechanisms underlying the success or failure of population regulation are to be understood.

Acknowledgements

References

Agrawal, A.A. (1997) Do leaf domatia mediate a plant-mite mutualism? An experimental test of the effects on predators and herbivores. *Ecological Entomology*, **22**, 371–376.

Agrawal, A.A. & Karban, R. (1997) Domatia mediate plant–arthropod mutualism. *Nature*, **387**, 562–563.

Agrawal, A.A., Karban, R. & Colfer, R.G. (2000) How leaf domatia and induced plant resistance affect herbivores, natural enemies, and plant performance. *Oikos*, **89**, 70–80.

Chesson, J. (1989) The effect of alternative prey on the functional response of *Notonecta hoffmani*. *Ecology*, **70**, 1227–1235.

Cloyd, R.A. & Sadof, C.S. (2000) Effects of plant architecture on the attack rate of *Leptomastix dactylopii* (Hymenoptera: Encyrtidae), a parasitoid of the citrus mealybug (Homoptera: Pseudococcidae). *Environmental Entomology*, **29**, 535–541.

De Clercq, P., Mohaghegh, J. & Tirry, L. (2000) Effect of host plant on the functional response of the predator *Podisus nigrispinus* (Heteroptera: Pentatomidae). *Biological Control*, **18**, 65–70.

Donnelly, B.A. & Phillips, T.W. (2001) Functional response of *Xylocoris flavipes* (Hemiptera: Anthocoridae): effects of prey species and habitat. *Environmental Entomology*, **30**, 617–624.

Evans, H.F. (1976) The searching behaviour of *Anthocoris confuses* (Reuter) in relation to prey density and plant surface topography. *Ecological Entomology*, **1**, 163–169.

Gleick, J. (1987) *Chaos: Making of a New Science*. Penguin Books Ltd, New York.

Hawkins, B.A., Thomas, M.B. & Hochberg, M.E. (1993) Refuge theory and biological control. *Science*, **262**, 1429–1432.

Hoddle, M.S. (2002) The developmental and reproductive biology of *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae). *Bulletin of Entomological Research*, **92**, 279–285.

Hoddle, M.S., Jones, J., Oishi, K., Morgan, D. & Robinson, L. (2001a) Evaluation of diets for the development and reproduction of *Franklinothrips orizabensis* (Thysanoptera: Aeolothripidae). *Bulletin of Entomological Research*, **91**, 273–280.

Hoddle, M.S., Oishi, K. & Morgan, D. (2001b) Pupation biology of *Franklinothrips orizabensis* (Thysanoptera: Aeolothripidae) and harvesting and shipping of this predator. *Florida Entomologist*, **84**, 272–281.

Hoddle, M.S., Robinson, L., Drescher, K. & Jones, J. (2000) Developmental and reproductive biology of a predatory *Franklinothrips* n. sp. *Biological Control*, **18**, 27–38.

Hoddle, M.S., Van Driesche, R.G., Elkinton, J.S. & Sanderson, J.P. (1998) Discovery and utilization of *Bemisia argentifolii* patches by *Eretmocerus eremicus* and *Encarsia formosa* (Beltsville strain) in greenhouses. *Entomologia experimentalis et applicata*, **87**, 15–28.

Ives, A.R., Kareiva, P. & Perry, R. (1993) Response of a predator to variation in prey density at three hierarchical scales: lady beetles feeding on aphids. *Ecology*, **74**, 1929–1938.

Juliano, S.A. (1993) Non-linear curve fitting: predation and functional response curves. *Design and Analysis of Ecological Experiments* (ed. by S. M. Scheiner and J. Gurevitch), pp. 158–183. Chapman & Hall, New York.

Juliano, S.A. & Williams, F.M. (1987) A comparison of methods for estimating the functional response parameters of the random predator equation. *Journal of Animal Ecology*, **56**, 641–653.

Kaiser, H. (1983) Small scale spatial heterogeneity influences predation success in an unexpected way: model experiments on the functional response of predatory mites (Acarina). *Oecologia*, **56**, 249–256.

Kareiva, P. (1987) Habitat fragmentation and the stability of predator–prey interactions. *Nature*, **326**, 388–390.

Kareiva, P. & Perry, R. (1989) Leaf overlap and the ability of ladybird beetles to search among plants. *Ecological Entomology*, **14**, 127–129.

Kareiva, P. & Sahakian, R. (1990) Tritrophic effects of a simple architectural mutation in pea plants. *Nature*, **345**, 433–434.

Lewis, T. (1973) *Thrips: their Biology, Ecology and Economic Importance*. Academic Press, London.

McMurtry, J.A., Johnson, H.G. & Newberger, S.J. (1991) Imported parasite of greenhouse thrips established on California avocado. *California Agriculture*, **45**, 31–32.

Messina, F.J. & Hanks, J.B. (1998) Host plant alters the shape of the functional response of an aphid predator (Coleoptera: Coccinellidae). *Environmental Entomology*, **27**, 1196–1202.

Morse, J.G., Bellows, T.S., Jr & Iwata, Y. (1986) Technique for evaluating residual toxicity of pesticides to motile insects. *Journal of Economic Entomology*, **79**, 281–283.

Neuenschwander, P. & Ajuonu, O. (1995) Measuring host finding capacity and arrestment of natural enemies of the cassava mealybug, *Phenococcus manihoti*, in the field. *Entomologia experimentalis et applicata*, **77**, 47–55.

Norton, A.P., English-Loeb, G. & Belden, E. (2001) Host plant manipulation of natural enemies; leaf domatia protect beneficial mites from insect predators. *Oecologia*, **126**, 535–542.

Parajulee, M.N., Phillips, T.W. & Hogg, D.B. (1994) Functional response of *Lyctocoris campestris* (F.) adults: effects of predator sex, prey species, and experimental habitat. *Biological Control*, **4**, 80–87.

Ritchie, M.E. (1998) Scale-dependent foraging and patch choice in fractal environments. *Evolutionary Ecology*, **12**, 309–330.

Rogers, D. (1972) Random search and insect population models. *Journal of Animal Ecology*, **41**, 369–383.

Ryoo, M.I. (1996) Influence of the spatial distribution pattern of prey among patches and spatial coincidence on the functional and numerical response of *Phytoseiulus persimilis* (Acarina, Phytoseiidae). *Journal of Applied Entomology*, **120**, 187–192.

SAS Institute (1990) *SAS/STAT User's Guide: Statistics, Version 6*. Cary, North Carolina.

Smith, P. (1998) *Explaining Chaos*. Cambridge University Press, Cambridge.

Solomon, M.E. (1949) The natural control of animal populations. *Journal of Animal Ecology*, **18**, 1–35.

Trexler, J.C., McCulloch, C.E. & Travis, J. (1988) How can the functional response best be determined? *Oecologia*, **76**, 206–214.

Trexler, J.C. & Travis, J. (1993) Nontraditional regression analyses. *Ecology*, **74**, 1629–1637.

Walter, D.E. (1996) Living on leaves: mites, tomenta, and leaf domatia. *Annual Review of Entomology*, **41**, 101–114.

Walter, D.E. & O'Dowd, D.J. (1992) Leaves with domatia have more mites. *Ecology*, **73**, 1514–1518.

Williams, F.M. & Juliano, S.A. (1996) Functional response revisited. *Environmental Entomology*, **25**, 549–550.