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FUNCTIONAL RESPONSE OF *CURINUS COERULEUS* (*COL.: COCCINELLIDAE*) TO *HETEROPSYLLA CUBANA* (*HOM.: PSYLLIDAE*) ON ARTIFICIAL AND NATURAL SUBSTRATES

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Laboratory measurements of the functional response of adult *Curinus coeruleus* (Mulsant) to nymphs of *Heteropsylla cubana* Crawford on filter paper and on leaves of different host plants showed a significant effect of these different substrates on nymph consumption at several different densities. Moreover, this effect may be explained by the influence of the substrate on the search rate of the predator. Host plants tested included *Leucaena leucocephala* (Lam) de Witt, *L. diversifolia* (Schlecht.) Benth. and *L. pallida* Britton and Rose.

Results obtained may be relevant to plant-protection research programs involving the integration of biological control with host-plant resistance.

KEY-WORDS: Functional response, *Curinus coeruleus, Heteropsylla cubana, Leucaena leucocephala,* biological control, host-plant resistance.

A traditional approach to studying the impact of insect predators on their prey has been an analytical one, in which the total response of the entomophagous species is initially decomposed into two parts, the functional response and the numerical response (**Solomon,** 1949), each of which in turn may be considered to have its own subcomponents. Study of how selected components of the functional response are affected by various characteristics of the predators, the prey and their background environment has provided valuable insight into the overall process of predation (**Holling,** 1959 ; **Holling,** 1961 ; **Hagen** *et al.* 1976 ; **Luff,** 1983 ; **Luck,** 1985). However, in general, characteristics of the plants on which insect predators forage have not received much attention in functional response studies.

Nevertheless, more information about the effects of plant characteristics on predator-prey interactions is needed to promote better integration of biological control techniques with those of host-plant resistance. Although many plant characteristics have been proposed as potentially important in the maintenance of that resistance that depends on the action of natural enemies, termed extrinsic resistance (**van Emden & Way,** 1972 ; **Bergman & Tinney,** 1979 ; **Price,** 1986 ; **Obrycki,** 1986 ; **Hagen,** 1986 ; **Kareiva & Sahakian,** 1990), the effects of these characteristics are often difficult to test in the field. However, in case of structural characteristics, the laboratory functional response test, though originally conceived to answer purely theoretical questions, may also serve as a useful bioassay in the initial stages of investigation of extrinsic resistance.

The following experiment was conducted to measure the functional response of *Curinus coeruleus* (Mulsant) to *Heteropsylla cubana* Crawford on different substrates thought to be important under field condition. It was hypothesized that structural differences in the substrates were important enough in the predation process to be reflected in the functional response observed.

Both of the insects studied are currently the subject of considerable attention. *Heteropsylla cubana,* the leucaena psyllid, is a serious pest of the widely-planted tree *Leucaena leucocephala* (Lam) de Wit, and much effort is presently being devoted to find methods of controlling it, especially in Southeast Asia and the Pacific (**Waterhouse & Norris,** 1987).

Although some uncertainty exists regarding its importance as a mortality factor, it is generally agreed that *C. coeruleus* feeds readily on *H. cubana.* While it does not seem by itself to be capable of bringing about satisfactory control in all areas, it has responded conspicuously to psyllid outbreaks (**Nakahara** *et al.,* 1987 ; **Funasaki** *et al.,* 1989) and has been introduced into several countries as a biological control agent (**Waterhouse & Norris,** 1987 ; **Napompeth,** 1989). Predation by *Curinus* has been reported as an important factor in observed plant resistance (**Sorensson & Brewbaker,** 1987 ; **Wheeler,** 1988).

MATERIALS AND METHODS

Adult female *C. coeruleus* were collected from *L. leucocephala* in plantings at the University of Hawaii Agricultural Experiment Station, Waimanalo, Oahu, during a psyllid outbreak in June, 1989. The beetles were removed to the laboratory, where each was placed in an individual separate glass vial and held for 24 h without feeding. At the end of this period they were introduced into plastic vials 8 cm long and 2.5 cm in diameter and containing selected numbers of late-instar psyllid nymphs distributed on the substrates described below. The nymphs had been freshly collected at the same field site as the beetles and were introduced so as to provide densities ranging from 10 to 70 per vial. All nymphs were allowed to distribute themselves freely over the substrates before introduction of the beetles. After the introduction of the beetles, the vials were sealed and laid on their sides in an area with natural lighting from a large window. The beetles were allowed to feed undisturbed for 24 h. At the end of this time, the beetles were removed, and the nymphs remaining in each vial were counted. No beetle was used more than once. Each beetle was weighed immediately before and after its use in a feeding trial. Small samples of representative nymphs were also weighed. Ambient temperature during all trials was 23 °C.

Beetles were randomly assigned to combinations of 7 levels of nymph density and 5 substrate treatments. Each combination was replicated 7 times.

Treatments included one « artificial » and four « natural » substrates. The artificial substrate, Treatment A, was a strip of moistened filter paper, 6 cm × 1 cm, glued to the lower surface of the vial. The natural substrates, Treatments B, C, D, and E, were pairs of terminals pinnae (primary leaflets), also cut to 6 cm in length, from the pinnately compound leaves of *Leucaena* plants. These were provided in small glass vials filled with moistened cotton and inserted into the larger vials through holes made for this purpose so that only the leaflet surfaces were left exposed to the insects. In the experimental set-up, all pinnae opened and closed according to the same diurnal rhythm as in the field.

Each of the « natural » treatments contained leaflets from accessions of *Leucaena* represented in the psyllid resistance trials conducted by the Nitrogen-Fixing Tree Association at the same site where the insects were collected. All of these plants supported populations of *Heteropsylla,* but differed greatly in amounts of observed damage.

Treatments B and C used leaflets from « K8 », a variety of *L. leucocephala.* Treatment D used leaflets from « K784 », an accession of *L. diversifolia* (Schlecht.) Benth., while leaflets for Treatment E came from plants of « K376 », an accession of *L. pallida* Britton and Rose. Descriptions of species and accession of *Leucaena* are given in **Brewbaker** (1987) and **Wheeler** (1988). All leaves chosen were the youngest of full size on their respective shoots, except those in Treatment C, which were taken from positions one node up the shoots from the youngest full-sized leaves, and hence were slightly younger than the rest.

Pinnae in each treatment had a characteristic geometry. Pinnae from different treatments, however, differed in the ways in which they were subdivided into pinnules (secondary leaflets). Some pinnae were composed of few, relatively wide pinnules, while others had many, relatively narrow pinnules. Since all pinnae were of the same length, this inverse variation in width and number of pinnules, minimized differences in total leaf surface area between treatments.

RESULTS

All treatments showed the same general pattern of response, as shown in fig. 1. However, there was a strong treatment effect on consumption. Separate one-way analyses of variance showed treatment effects to be significant at the 95 % level at 4 of the 7 densities tested (table 1). There also seemed to be some consistency across densities in the ranking of the treatments, with Treatments A and D always showing the highest nymph consumption. Absolute maximum consumption for the 24 hour period was 63 nymphs.

TABLE 1

Mean numbers of Heteropsylla cubana *nymphs consumed by adult* Curinus coeruleus *in 24 hr on five different substrates. Means followed by the same letter are not significantly different according to Fisher's PLSD test ($P > 0.05$)*

Density	Treatment	Prey Consumed $\bar{x}$		S.E.	« p-value » one-way ANOVA
10	A	9.57	a	0.20	0.004
10	D	8.29	a b	0.78	
10	B	5.86	b c	1.35	
10	E	5.00	c	0.93	
10	C	4.43	c	1.31	
20	D	17.14	a	1.22	0.0004
20	A	16.86	a	1.18	
20	C	11.71	b	0.75	
20	E	11.71	b	1.49	
20	B	8.71	b	1.91	
30	A	24.71	a	1.44	0.139
30	D	23.00	a	1.41	

Density	Treatment	Prey Consumed $\bar{x}$		S.E.	« p-value » one-way ANOVA
10	A	9.57	a	0.20	0.004
30	C	20.29	a	2.97	
30	B	17.71	a	2.93	
30	E	17.00	a	2.78	
40	D	30.57	a	2.75	0.094
40	A	26.00	a	3.12	
40	B	22.57	a	2.98	
40	E	20.14	a	2.47	
40	C	19.43	a	3.99	
50	D	39.29	a	3.16	0.008
50	A	36.57	a	2.60	
50	C	25.86	b	4.07	
50	B	25.29	b	3.66	
50	E	23.57	b	4.01	
60	D	42.29	a	3.05	0.662
60	A	39.29	a	6.47	
60	E	37.86	a	4.95	
60	C	36.00	a	5.68	
60	B	32.43	a	2.00	
70	D	39.57	a	4.23	0.011
70	A	38.14	a b	2.73	
70	E	34.29	a b	3.01	
70	C	30.14	b c	3.33	
70	B	24.00	b c	2.24	

There was a net gain in weight for most beetles during the experiment. For the 212 beetles for which weights were obtained, the mean weight gain per nymph consumed was 0.07 ± 0.006 mg, or 0.54 ± 0.045 percent. Mean beetle weight was 15.8 ± 0.28 mg immediately before the experiment and, for a sample of 40, mean nymph weight was 0.15 ± 0.012 mg.

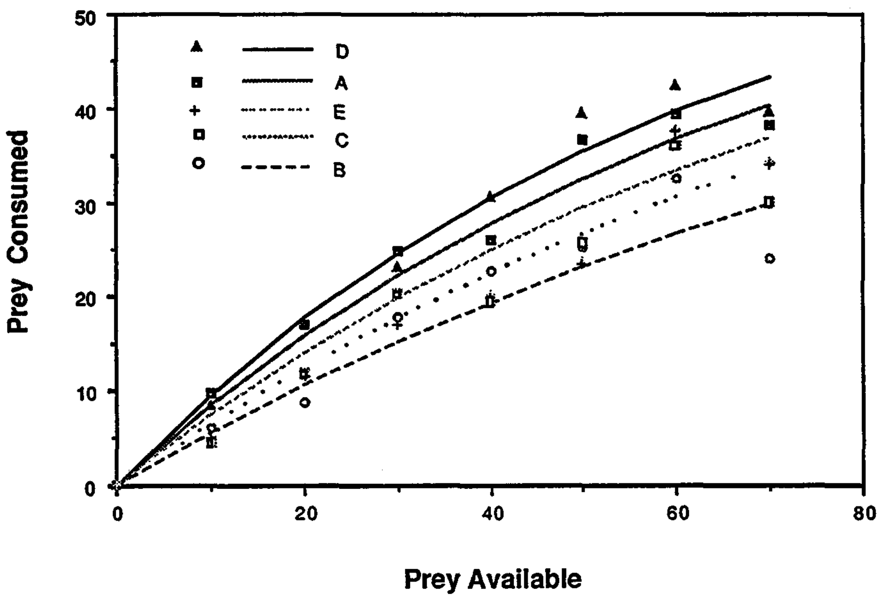

Fig. 1. Functional response of *Curinus coeruleus* Mulsant to *Heteropsylla cubana* Crawford on five different substrates. Mean numbers of nymphs consumed are indicated by symbols, while curves predicted by the Frazer-Gilbert model are indicated by lines. Letters correspond to the five treatments : A. Filter Paper, B. *L. leucocephala* (older), C. *L. leucocephala* (younger), D. *L. diversifolia*, E. *L. pallida*.

Age probably varied widely in the field-collected beetles. Death of 5 beetles, necessitating their replacement, may have been due to old age.

DISCUSSION

Differences between treatments reflect effects of the substrates used ; they may be the result of different levels of « protection » provided. It was observed that after exposure to the pinnae, almost all nymphs settled into spaces between and near the bases of the pinnules. These spaces appeared most protected in the pinnae from the plants with the broadest pinnules, *L. leucocephala* (Treatments B and C), and least protected in the pinnae from the plant with the narrowest pinnules, *L. diversifolia* (Treatment D). The filter papers of Treatment A may be considered to be « artificial pinnae » offering no protected spaces at all. The protection effect appeared most pronounced when pinnae were partially closed. However, even when pinnae were fully open, nymphs seemed to evade the predators most easily by moving to the opposite side of a large pinnule. In addition, the spaces between pinnule edges in fully-opened pinnae happened to be smaller where pinnules were narrower. Thus, predators could more easily walk directly from one pinnule to another on these pinnae. On pinnae of treatments employing wider pinnules, much of the beetles' time was spent on the rachis, a behavior that has been reported for other coccinellids on plants with large leaflets (**Marks**, 1977).

The importance of all of these differences in leaf form appears to be accentuated by these predators' reliance on tactile rather than visual cue in locating their prey. The beetles seemed unaware of their prey until contact was made, usually with the maxillary palps. This behavior has been reported for other coccinellids (**Kesten**, 1969).

Further insight into the results obtained may be gained by comparing them with those predicted by the predator form (**Gutierrez** *et al.*, 1981) of the Frazer-Gilbert functional response model (**Frazer & Gilbert**, 1976). According to this model,

$$N_a = b(1 - e^{-SN/b}), \tag{1}$$

where N_a = observed or expected predation, b = maximum predation, considered to be determined by hunger or physiological demand, N = number of prey available, and S = proportion of area searched by a predator following a random path.

All of the parameters required by the model can be obtained from the available data. The maximum level of consumption observed in this experiment, 63 nymphs, which is essentially the same as those observed elsewhere (**Maneeratana**, 1989), can provide an estimate for the value of b in this equation. Values for s in each treatment can be computed as the slopes of linear regressions which utilize the values for consumption obtained at the different prey densities, as well as the following rearranged form of the basic equation :

$$- b \ln [(b - Na)/b] = SN \tag{2}$$

The curves predicted by the model are also shown in fig. 1, superimposed upon the results obtained in the feeding trials. The form of each curve is the same, coinciding with the experimental data, except at the highest prey density, where a conspicuous decrease in consumption was observed. This was perhaps due to predator confusion, which is not accounted for in the model.

More of interest here are the differences between the model-generated curves themselves. These differences are caused entirely by differences in the search parameter s used in the computations. This parameter assumes its smallest values in Treatments B and C, those of the widest pinnules. It has an intermediate value in Treatment E, while it approaches its maximum for Treatments A and D, the two treatments in which the beetles perceived no barriers to lateral (pinnule to pinnule) movement. In fact, for the treatments using leaves (B-D), S may be shown to be related to the average pinnule width w by the equation

$$S = 1.08/w^{0.606} \; (r^2 = 0.997) \tag{3}$$

The search parameter may thus provide a good measure of the « protection » (or lack of it) on a given substrate type, and, in the present example, this appears to be dependent on the width of the pinnules of the leaves upon which the beetles forage (fig. 2).

The model may be modified to reflect the influence of pinnule width. This is done by combining Equations 1 and 3 to give the equation

$$N_a = b[1 - e^{(-1.08N)/(bw^{0.606})}], \tag{4}$$

which predicts the consumption (N_a) expected at different prey densities (N) and pinnule widths (w). The expected consumption levels produced by this more general model are shown in fig. 3.

The fit of Equation 4 to the data is very good. The coefficient of multiple determination (R^2) is 0.94, while the slope of a simple regression line constructed with a composite of N and w and the observed values of Na, according to the following rearrangement of Equation 4,

$$\ln [(b - Na)/b] = - 1.08/b \, (N/w^{-0.606}), \tag{5}$$

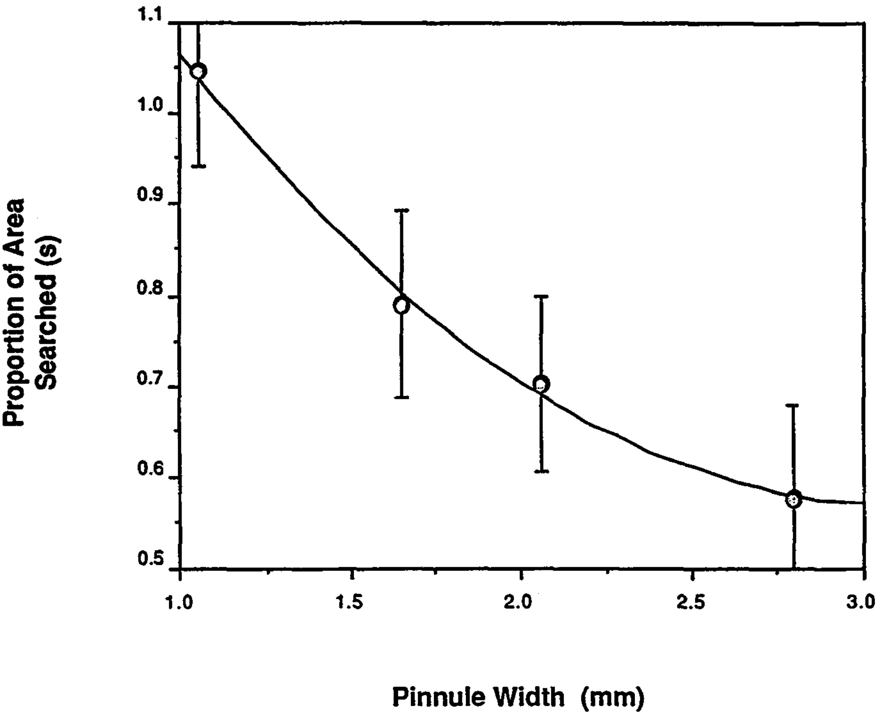

Fig. 2. Relation of pinnule width (w) to proportion of area searched (s). Curve is given by Equation 3.

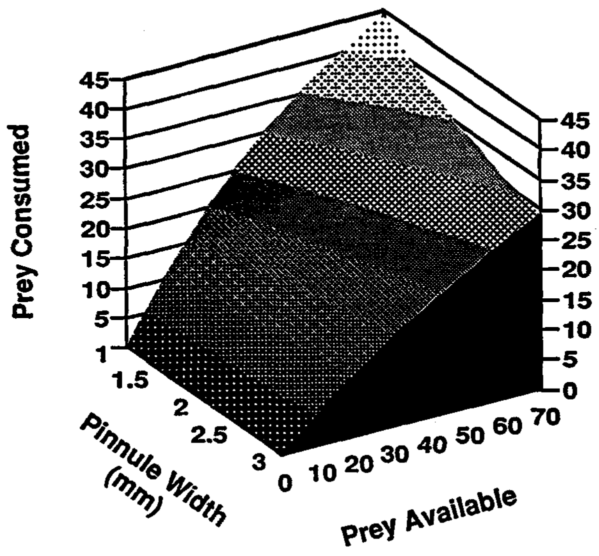

Fig. 3. Functional response of *Curinus coeruleus*. Response surface is generated from Equation 4.

is − 0.17, with a standard error of 0.0096, virtually identical to the value of − 1.08/b predicted by the model. To our knowledge, this is the first attempt to use a parameter related to the shape of the substrate as a predictor for s, although an attempt had been made previously to improve the Frazer-Gilbert model in a parallel way by making s a function of other variables, predator size and leaf area index (**Gutierrez** *et al.*, 1988).

In conclusion, the following thoughts are offered regarding the utility of the functional response data in answering questions of interest about *C. coeruleus, H. cubana,* and *Leucaena.*

That the simple set of experiments reported here was able to detect the effects of differences of plant structure on the predator's impact on the prey supports the hypothesis that these differences are important to the predation process and suggests that they may have a significant impact on biological control. It also indicates that at least some measurement of extrinsic resistance can be made rapidly in the laboratory, separately from measurements of intrinsic resistance. Tests of this type may be useful in plant breeding programs.

Of course it must be remembered that this study, as other laboratory studies, represents a simplification of a natural system. Only selected stages of the insects and selected parts of the plants were used. It remains to be seen whether other stages of the insects interact according to the same patterns and what other environmental influences operating at the whole-plant scale have important effects on these interactions. Studies of the functional response at the latter scale have recently been carried out (**O'Neill**, 1989) ; more of these would seem to be worthwhile.

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RÉSUMÉ

Réponse fonctionnelle de *Curinus coeruleus (Col. : Coccinellidae)* à *Heteropsylla cubana (Hom. : Psyllidae)* sur des substrats artificiels et naturels.

Des résultats obtenus en laboratoire sur la réponse fonctionnelle des adultes de *Curinus coeruleus* (Mulsant) aux nymphes de *Heteropsylla cubana* Crawford sur des substrats differents ont révélé un effet significatif du substrat sur l'ingestion des nymphes à différents densités. Les substrats utilisés étaient composés de matière foliaire de *Leucaena leucocephala* (Lam) de Wit d'espèces apparentées en plus d'un substrat de papier comme témoin.

Les résultats obtenus pourraient être utiles en ce qui concerne des projets intégrant lutte biologique et sélection de variétés résistantes.

MOTS CLÉS : Réponse fonctionnelle, *Curinus coeruleus, Heteropsylla cubana, Leucaena leucocephala,* lutte biologique, variétés résistantes.

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