

Functional Response of *Anisopteromalus calandrae* (Hymenoptera: Pteromalidae): Influence of Host Numbers Versus Host Density¹

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ABSTRACT The functional response of *Anisopteromalus calandrae* (Howard) was measured on rice weevil, *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae), in wheat at 30°C. Four female parasitoids, with males, were allowed to oviposit during their lifespan on 166 to 678 weevils per container. The data were fit by Rogers' (1972) random parasitoid model with rate of parasite search $a' = 0.32$ lifespan⁻¹ and handling time $T_h = 0.0027$ lifespan. Volume of grain, in the range of 0.19 to 3.1 l wheat, had no effect on number of hosts parasitized when host numbers were held constant at 222, 398, and 572 weevils per container. Therefore, it may be more appropriate to consider numbers of hosts present rather than host density when studying functional response within a patch of uniformly distributed hosts.

KEY WORDS Functional response, parasitoid, biological control, rice weevil, stored product, wheat.

Anisopteromalus calandrae (Howard) is a cosmopolitan, solitary parasitoid of immature rice weevils, *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae), and other beetles that develop inside kernels of stored grains and legumes (Chatterji 1955). Laboratory studies have demonstrated the potential of *A. calandrae* to suppress populations of rice weevil in stored wheat (Press et al. 1984; Cline et al. 1985). However, the use of *A. calandrae* as an economically efficient biological control agent of the rice weevil depends on our ability to predict the number of parasitoids to release. Functional response data can be used to help predict the number of hosts killed as a function of host density.

Functional response has traditionally been studied by varying the number of hosts in an arena of constant area (e.g., Houck and Strauss 1985). However, it is not clear that host numbers and arena area have exactly reciprocal effects on rate of attack. The question of arena size is particularly important when experimental studies are intended to simulate parasitoid behavior at low host densities, such as those dictated by economic injury levels. Arena size can have a substantial effect on the cost of performing such experiments, so it would be useful to determine the significance of its effect on parasitism at the spatial scale proposed for a particular experiment.

The purpose of this study was to measure the functional response of *A. calandrae* on rice weevil in wheat, and to determine the importance of host density (insects per volume or surface area) versus actual numbers of hosts available.

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Materials and Methods

Anisopteromalus calandrae came from a ten year old laboratory culture maintained on rice weevil in wheat, which had been established from adults collected on wheat in Savannah, GA. Stock cultures of rice weevils were produced by ca. 300 adults ovipositing for 3 d on 300 g soft red winter wheat (12% moisture content). Stock cultures were incubated at 30°C for 23 d (to produce large larvae), mixed, and 100 g portions were combined with uninfested wheat to produce uniformly mixed samples of 150, 300, 600, 1200, and 2400 g (194, 388, 776, 1,552, 3,105 ml, respectively). These samples were placed in glass canning jars (237, 474, 948, 1,895, 3,790 ml, respectively) closed with screen lids sandwiched between two pieces of filter paper. Four pairs of *A. calandrae* adults 0 to 24-h-old were placed in each jar and held at 30°C, 60% RH, and a photoperiod of 12:12 h L:D for 21 d (sufficient time for P_1 generation to die and all F_1 progeny to emerge), and then frozen. Four pairs were used to allow intraspecific interactions to occur among foraging females and between sexes, as might occur during inundative releases (e.g., Rogers and Hassell 1974; Beddington 1975). All emerged *A. calandrae* and rice weevil adults were counted, and the eight initial parasitoids were subtracted. Three replicates of control (no *A. calandrae*) and experimental jars were set up for each quantity of grain, and the experiment was performed three times. The density of weevils in the stock culture differed on the three dates as described below.

Statistical Methods. The combined number of *A. calandrae* and rice weevils emerged was regressed against number of rice weevils emerged in controls to determine whether the former was a good estimate of the number of hosts available.

Rogers' (1972) random parasitoid model was used to fit the functional response data:

$$N_a = N \left[1 - \exp \left(\frac{-a' TP}{1 + a' T_h N} \right) \right]$$

where N_a is the number of hosts parasitized; N , the number of hosts available; a' , the rate of parasitoid search; P , the number of female parasitoids; T , the duration of the experiment; and T_h , the handling time per host. This model assumes random search behavior, no discrimination of previously parasitized hosts (i.e., handling time for both types of hosts is the same [Arditi 1983]), and constant host population during the time interval (Rogers 1972). Unweighted nonlinear regression was used to calculate estimates for a' and T_h (Proc NLIN with the DUD multivariate secant method of iteration [SAS Institute 1988]; see also Juliano and Williams 1987). Values for P and T were defined by experimental conditions: $P = 4$ and $T = 1$ (adult lifespan; units of days were not used because time of death was not observed); however, mean female longevity at 30°C is 7 to 12 d (Ghani 1943; Smith 1992) and 79 to 99% of oviposition is completed by 8 d (Ghani and Sweetman 1955; Smith 1992). Adequacy of the model was evaluated by examining residuals plotted against predicted values, number of hosts, grain volume, and date, and by comparing the mean squares ratio (lack of fit MS/pure error MS) to the F statistic (Draper and Smith 1981). The effect

of grain volume and date were examined by adding linear terms for each to the random parasitoid model and evaluating the extra SS attributed to these parameters (Bates and Watts 1988). The effect of grain volume alone (i.e., host density, independent of host numbers) was investigated by performing a linear regression of number of emerged *A. calandray* on volume, while blocking for replication date (Proc GLM [SAS Institute 1988]).

Results and Discussion

The mean number of rice weevils emerged per control sample on the three experimental dates was: 571.8 (15.4 SE), 222.5 (4.7), and 397.7 (14.1). Combined number of *A. calandray* and rice weevil emerged per experimental sample was 566.0 (9.3), 205.5 (5.3), and 388.9 (8.1), respectively.

Regression of the combined number of emerged *A. calandray* and rice weevils against the number of emerged rice weevils in controls indicates a one-to-one correspondence ($Y = 0.998 [\pm 0.032 \text{ SE}] X - 9.85 [\pm 13.50]$; $F = 982.2$, $df = 1, 43$, $P = 0.0001$, $r^2 = 0.958$; test of H_0 slope = 1.0: $F = 0.0035$, $df = 1, 43$, $P = 0.95$; test of H_0 intercept = 0.0: $F = 0.533$, $df = 1, 43$, $P = 0.47$; Fig. 1). The slope (1.0) and the y -intercept (0.0) suggest that *A. calandray* did not cause any significant mortality of rice weevils other than by successful parasitism (mean difference of control emergence minus combined emergence was 2.5 ± 9.3 [95% CI]). Therefore, combined numbers of *A. calandray* and rice weevils emerging from samples were used to estimate initial numbers of hosts for the following analyses. However, Hassell et al. (1985) observed that 5.8% of *Callosobruchus maculatus* (F.) in black-eyed beans produced neither an adult host nor parasitoid when exposed to *A. calandray*, so our estimates of host numbers may be low. The precision of our data would not permit detection of host mortality less than 6.4% (95% CI of the estimated slope).

The functional response of *A. calandray* on rice weevil in wheat is presented in Fig. 2. The random parasitoid model (Rogers 1972) provided an adequate fit to the data ($a' = 0.32 \pm 0.10$ [asymptotic 95% CI] lifespan⁻¹ [unspecified time period], $T_h = 0.0027 \pm 0.0019$ lifespan; $r^2 = 0.894$; pure error MS = 838.7, $df = 20$; lack of fit MS = 825.0, $df = 23$; mean squares ratio = 0.98, which is less than $F = 2.04$, $df = 20, 23$, $\alpha = 0.05$). Residuals were well-behaved when plotted against the predicted values or any of the independent variables. Grain volume and date (host numbers) were not significant when added separately to the nonlinear regression model as linear variables (analysis of extra SS, Table 1).

Grain volume also had no significant effect on number of parasitoids emerged when regressed after blocking for experimental date (host numbers differed between dates but were constant within dates) (Table 2, overall model; Fig. 3, individual regression models: date 1, $Y = 11.3 [\pm 9.3 \text{ SE}] X + 309.8$, $F = 1.47$, $df = 1, 13$, $P > 0.24$; date 2, $Y = 6.6 [\pm 4.3] X + 120.9$, $F = 2.33$, $df = 1, 13$, $P > 0.15$; date 3, $Y = 8.0 [\pm 9.2] X + 242.3$, $F = 0.76$, $df = 1, 13$, $P > 0.40$; where X is volume of grain in liters). Although each of the three regression equations has a positive slope, none of them are significantly different from zero ($\alpha = 0.05$). This indicates that in the range of 48 ml (37.5 g) to 776 ml (600 g) wheat per female parasitoid, grain volume had no significant effect on the number of hosts parasitized.

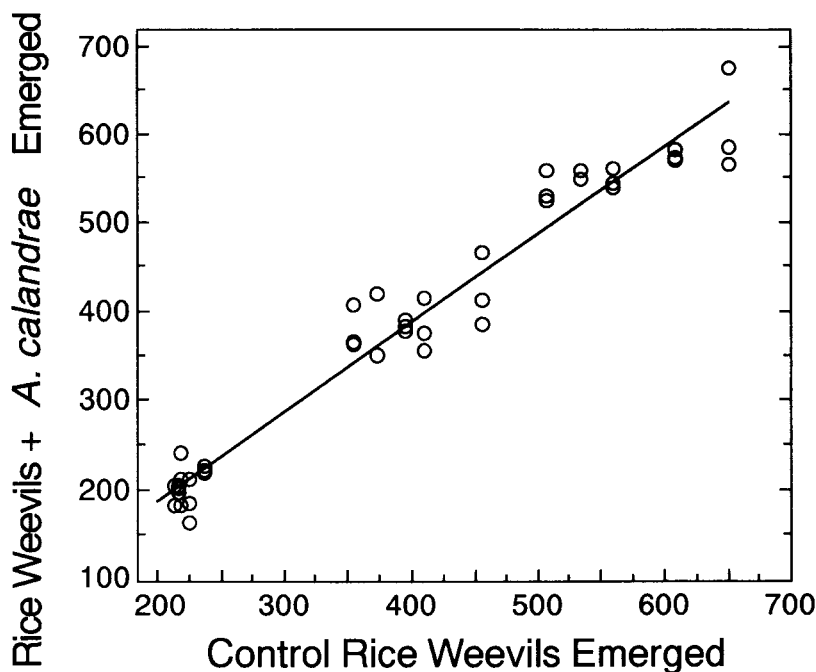


Fig. 1. Regression of combined number of rice weevils and *Anisopteromalus calandrae* emerged in experimental samples on number of rice weevils emerged in control samples ($Y = 0.998X - 9.85$; $r^2 = 0.958$; $n = 45$).

Ghani and Sweetman (1955) observed female *A. calandrae* producing an average of 121 progeny on rice weevil in wheat at 30°C, 3 mm saturation deficit (72% RH). Here we observed ≤ 95.5 progeny per female over her life ($\bar{x} = 80.9$ at 572 hosts), which is substantially lower than that observed by Ghani and Sweetman (1955). The slope at 700 hosts suggests that we were far from attaining maximum fecundity.

A decrease in number of suitable hosts, due to parasitism, during the experiment would violate the assumption of constant host population made in Rogers' (1972) random parasitoid model. This would cause us to underestimate a' , the attack rate, but it would not undermine conclusions regarding the effect of grain volume and host numbers because all treatments would be affected similarly. However, the hosts involved were distributed over a wide range of age and size classes (L. S. unpublished data). Small hosts, which are unsuitable for parasitism (Okamoto 1972; L. S. unpublished data), would grow and become suitable during the course of the experiment. This tends to replace hosts that have become unsuitable by being parasitized or maturing into unsuitable stages. During the 8 d period (Smith 1992) when most of the parasitism occurred, the population of suitable hosts probably did not differ greatly. Furthermore, this simulates foraging conditions expected to occur in the field.

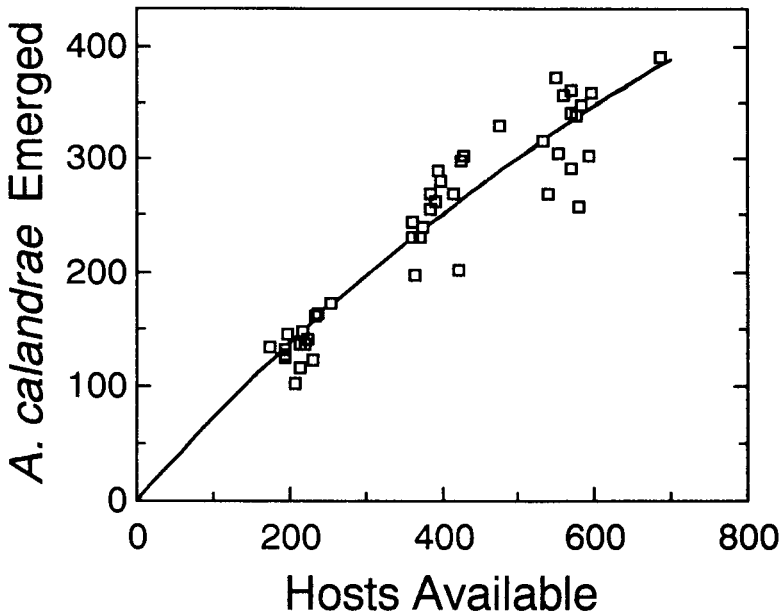


Fig. 2. Functional response of *Anisopteromalus calandray* on rice weevils in wheat fit by Rogers' (1972) random parasitoid model (for 4 pairs of adults over their lifespan at 30°C; $a' = 0.32$, $T_h = 0.0027$).

The proportion of rice weevils that escaped parasitism ranged from 32% at 200 hosts to 44% at 700 hosts per container. The low proportion of hosts parasitized in our experiment could be due to interference between the four adult females and males, which is known to reduce the rate of parasite search (Rogers and Hassell 1974; Beddington 1975; Abidi et al. 1989). It could also be due to some of the hosts being outside the suitable size range for parasitism (Okamoto 1972; Smith 1992), as discussed above.

This study indicates that the number of hosts parasitized by *A. calandray* is dependent upon the number of hosts available, rather than their density (hosts per volume or surface area), at this spatial scale. This suggests that functional response data collected from different-sized arenas will produce comparable model parameter estimates, provided the arena is not larger than the area that can be searched in the time available. Whether such conclusions would hold for a patchily-distributed host in a much larger environment (e.g., weevils in a commercial grain bin) may depend on how efficiently the parasitoid can locate host patches, relative to finding hosts within a patch. Such behavior is likely to involve a different mode of searching (i.e., different stimuli and locomotion). Although the larger spatial scale presents a serious challenge to experimentation, such knowledge is crucial for applying quantitative laboratory results to the development of effective biological control strategies.

Table 1. Evaluation of extra sums of squares to determine the significance of grain volume and experimental date, which were added as linear terms to the random parasitoid model.

Source	SS	df	MS	F
Extra parameter (Volume)	2	1	2	0.002*
Rogers Model + β_1 Volume [†]	35,989	42	857	
Rogers Model	35,991	43		
Extra parameter (Date)	3,389	3	1,130	1.39‡
Rogers Model + $\alpha_1 D_1 + \alpha_2 D_2 + \alpha_3 D_3$ [§]	32,602	40	815	
Rogers Model	35,991	43		

* *F* (ratio of extra parameter MS to full model MS) suggests lack of significance of Volume as an extra parameter if $F < F = 4.07$, $df = 1,42$, $\alpha = 0.05$.
† $\beta_1 = 0.15 \pm 4.09$ (asymptotic SE).
‡ *F* suggests lack of significance of Date as an extra parameter if $F < F = 2.84$, $df = 3,40$, $\alpha = 0.05$.
§ Indicator variables (D_1 - D_3) representing Date as a classification variable.

Table 2. Regression of parasitism by *Anisopteromalus calandrae* of rice weevils in wheat to determine the effect of grain volume (continuous variable) at three numbers of hosts per container (class variable) (see Fig. 3).

Source	df	Mean Square	F	P
Model	3	98,078.5	96.20	0.0001
Number of hosts	2	145,240.3	142.46	0.0001
Volume of grain	1	3,755.1	3.68	0.062
Error	41	1,019.5		

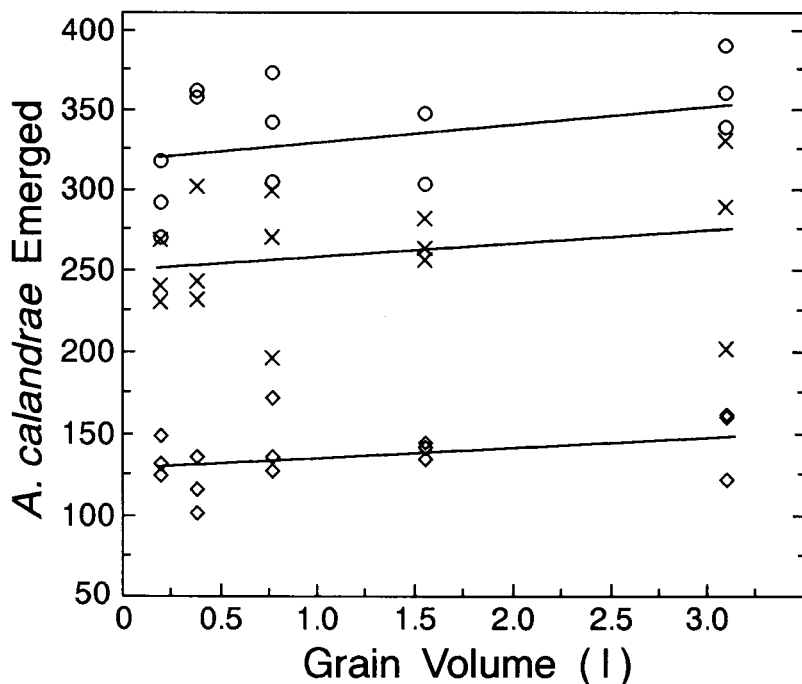


Fig. 3. Effect of grain volume on parasitism of rice weevils by *Anisopteromalus calandreae* for three numbers of hosts (\diamond , 222 ± 5 [SE]; \times , 398 ± 14 ; \circ , 572 ± 15 weevils per container). None of the regressions were statistically significant ($\alpha = 0.05$).

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