

Temperature-Dependent Functional Response of the Parasitoid *Cephalonomia waterstoni* (Gahan) (Hymenoptera: Bethylinidae) Attacking Rusty Grain Beetle Larvae (Coleoptera: Cucujidae)

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ABSTRACT The effects of host density and temperature on the functional response of the bethylid parasitoid *Cephalonomia waterstoni* (Gahan) attacking fourth-instar rusty grain beetle, *Cryptolestes ferrugineus* (Stephens) were examined. Five temperatures and six host densities were used. A type II functional response model was fit separately to each temperature. The maximum attack rate ranged from 7.5 larvae/12 h at 25°C, to 2.9 larvae/12 h at 38°C. Handling time and instantaneous search rate varied with temperature. A new functional response equation was developed in which handling time is a quadratic function of temperature. This equation explained 83% of the variation in attack rate. Although instantaneous search rate was also affected by temperature, it was sufficient to make only handling time a function of temperature because the two parameters were highly correlated.

KEY WORDS Insecta, biological control, *Cryptolestes ferrugineus*, functional response

THE RUSTY GRAIN BEETLE, *Cryptolestes ferrugineus* (Stephens), is one of the most abundant pests of farm-stored wheat in the United States (Hagstrum 1987). Adults and larvae feed primarily on the wheat germ and can cause considerable damage. *Cephalonomia waterstoni* (Gahan) is a hymenopteran parasitoid that is frequently found with the rusty grain beetle in stored grain (Sinha et al. 1979). This parasitoid may often prevent rusty grain beetle populations from reaching damaging levels (Hagstrum 1987) and may be potentially useful as a biological control agent.

Cephalonomia waterstoni is very host-specific (Finlayson 1950a,b). Although this wasp will parasitize larvae of other *Cryptolestes* species, it almost invariably prefers *C. ferrugineus* when given a choice. This wasp usually parasitizes only fourth instars; however, it will paralyze and feed on first through third instars (Rilett 1949). Earlier instars frequently feed within the wheat germ, where they are less likely to be attacked. In contrast, fourth instars are more vulnerable to attack because they move through the grain searching for pupation sites (Smith 1972). This wasp is an external parasitoid. After stinging the host, host paralysis occurs within 1 min. The wasp usually lays one to two eggs per host. It has a relatively low fecundity, laying an average of 2.3 eggs/d (Finlayson 1950a). In the experiment, the number of paralyzed hosts was counted rather than the number of hosts that had eggs attached to them. Paralyzation provides a better indication of the host finding ability of *C. waterstoni* than oviposition, because the wasp will paralyze many more hosts than it can oviposit on. The paralyzed larvae do not recover; thus, they remain suitable for oviposition for several weeks, even by other conspecifics.

The rate at which parasitoids attack hosts is dependent on host density. This relationship has been described as a functional response to host density (Solomon 1949). Temperature also affects functional response. There have been a limited number of studies investigating the effects of temperature on functional response (Burnett 1954, Messenger 1968, Everson 1980, Mack & Smilowitz 1982). Only Mack & Smilowitz (1982) have proposed a general model. In this study, I present a temperature-mediated functional response equation that uses a quadratic function for handling time. This model is used to predict attack rate as a function of host density and temperature.

Materials and Methods

Fourth-instar *C. ferrugineus* and adult *C. waterstoni* females were obtained from stock cultures at the U.S. Grain Marketing Research Laboratory in Manhattan, Kans. The wasp culture was ≈ 6 mo old. The adult parasitoids used in the experiments were ≈ 5 d old (adults live ≈ 3 wk at 30°C [Rilett 1949]). They had previous experience parasitizing *C. ferrugineus* larvae and were deprived of hosts for 24 h before the start of the experiment.

The arena consisted of glass jars (7.0 cm diameter, 13.5 cm tall) that contained 0.33 kg of wheat. The grain used in the studies was hard red winter wheat at 12% moisture; it was cleaned with a Hart-Carter Dockage Tester (Model XT2; Simon-Carter Company, Minneapolis, Minn.). To determine the effects of host density on parasitoid attack rate, either 0, 1, 2, 4, 8, 16, or 32 fourth-instar *C. ferrugineus* were placed on top of the wheat in each jar. The larvae moved down into the wheat almost immediately. A single 5-d-old adult *C. waterstoni*

Table 1. Estimates of instantaneous search rate, a , and handling time, T_h , for Royama (1971) and Rogers (1972) type II disk equation for parasitoids

Temp, °C	n	a (h^{-1}) \pm SE ^a	T_h (h) \pm SE ^a	R^2	P	Max no. paralyzed ^b
20	24	0.023 \pm 0.013	3.216 \pm 0.706	0.78	0.001	3.7
25	23	0.051 \pm 0.010	1.596 \pm 0.109	0.97	0.001	7.5
30	30	0.050 \pm 0.016	1.968 \pm 0.198	0.91	0.001	6.1
35	24	0.090 \pm 0.047	2.029 \pm 0.247	0.88	0.001	5.9
38	24	0.015 \pm 0.020	4.109 \pm 2.307	0.43	0.005	2.9

^a Asymptotic standard error.

^b Computed by dividing total time (12 h) by T_h .

female was introduced into each jar 8 h after the hosts were introduced. To determine the effect of temperature on functional response, tests were conducted in environmental chambers maintained at 20, 25, 30, 35, and 38 \pm 0.5°C and 75 \pm 5% RH in the dark. This represents the temperature range at which the parasite is able to develop and reproduce. A temperature of 40°C was used in preliminary experiments, but wasp mortality was >70% over a 12-h period. Temperatures lower than 20°C were not used because wasp larvae do not develop below that temperature (unpublished data). Each host density was replicated five times. Because all temperatures could not be run at the same time, temperatures were run in a random order. The insects were separated from the grain after 12 h using a 30-mesh sieve, and the numbers of paralyzed and unparalyzed larvae were recorded. Dead larvae were distinguished from paralyzed larvae by probing them with a fine-haired brush (paralyzed larvae moved when touched with a brush). There was no larval mortality during these experiments.

A type II disk equation for parasitoids (Royama 1971, Rogers 1972) was fit to the data:

$$N_a = N_t \left[1 - \exp \left\{ - \frac{aTP_t}{1 + aT_hN_t} \right\} \right] \quad (1)$$

where N_a is the number of hosts attacked, N_t are the number of hosts available, a is the instantaneous search rate, T is the total time of the experiment, P_t is the number of parasitoids and T_h is the parasitoid handling time. A nonlinear least squares program (Wilkinson 1989) was used to estimate the coefficients a and T_h , using a quasi-Newton method.

To develop a model that would predict functional response over a range of temperatures, a new functional response equation was developed in which a quadratic component that included temperature was substituted for handling time:

$$N_a = N_t \left[1 - \exp \left\{ - \frac{aTP_t}{1 + a(B_0 + B_1X + B_2X^2)N_t} \right\} \right] \quad (2)$$

where X is the temperature in degrees Centigrade and the other parameters are as previously de-

scribed. This four-parameter equation was fit to the entire data using a nonlinear least squares program (Wilkinson 1989) to estimate the coefficients a , B_0 , B_1 , and B_2 .

Results

Equation 1 was fit separately for each temperature (Table 1). The attack rate increased with host density at all of the temperatures tested. Instantaneous search rate was lowest at 20 and 38°C and was highest at 35°C. Estimated handling time was highest at 20 and 38°C and lowest at 25°C. The maximum paralyzation rate ranged from 7.5 larvae/12 h at 25°C to 2.9 larvae/12 h at 38°C.

To develop a model that would predict functional response over a range of temperatures, I investigated the relationship between estimated handling time and temperature. A plot of handling time versus temperature (not shown) indicated that a quadratic function was appropriate. A new functional response equation was developed in which a quadratic component that included temperature was substituted for handling time (equation 2). This four-parameter equation was fit to the entire data set using a nonlinear least squares program (Wilkinson 1989) to estimate the coefficients a , B_0 , B_1 , and B_2 . Estimates and SEs for a , B_0 , B_1 , and B_2 were 0.04797 \pm 0.0110, 19.918 \pm 0.849, -1.289 \pm 0.029, and 0.02266 \pm 0.0003, respectively. Equation 2 fit the data well ($R^2 = 0.83$; $F = 151.8$; $df = 4, 121$; $P < 0.0001$) for all temperatures except for 25°C, in which case it slightly underestimated paralyzation rate (Fig. 1). I also fit a four-parameter equation (not shown) that was similar to equation 1 except that instantaneous search rate was a quadratic function of temperature. This equation appeared to fit the data well ($R^2 = 0.84$; $F = 165.9$; $df = 4, 121$; $P < 0.0001$). However, at 20 and 38°C, it underestimated attack rate at low densities and overestimated attack rate at high densities. This systematic bias did not occur with equation 2. A six-parameter equation (not shown) was also fit to the data, in which both instantaneous search rate and handling time were quadratic functions of temperature ($R^2 = 0.85$; $F = 114.1$; $df = 6, 119$; $P < 0.0001$). Because the R^2 value was only slightly higher for the six-parameter equation, equation 2 was selected as the best model.

Discussion

Although both handling time and search rate varied in response to temperature, there are several reasons why it was sufficient to make only handling time a function of temperature. In this study, handling time and instantaneous search rate were correlated over the range of temperatures examined ($r = 0.76$, $P = 0.05$, $n = 5$). Thus, by making handling time a function of temperature, instantaneous search rate was also partially adjusted. In addition, handling time determines the host density at which the asymptote is reached; thus, it has a major effect on how the model fits the data. In contrast, instantaneous search rate primarily affects the shape of the functional response at low to intermediate host densities. Fitting the model in which only instantaneous search rate was a quadratic function of temperature resulted in a systematic bias in the estimated functional response at low and high host densities at the two temperature extremes. This systematic bias did not occur with equation 2.

Mack & Smilowitz (1982) developed a six-parameter temperature-mediated functional response model for *Coleomegilla maculata* (DeGeer) preying on green peach aphids, *Myzus persicae* (Sulzer). They used a four-parameter enzyme kinetics equation (Eyring & Urry 1975) to predict search rate as a function of temperature and a linear two-parameter equation for handling time. Theoretically, the relationship between handling time and temperature should be U-shaped because there should exist an optimum and two temperature extremes at which handling time is infinite (Mack et al. 1981). A quadratic function is a simple way to model this relationship. The advantage of the model developed in this study is that it incorporates a nonlinear temperature-mediated handling time that adds only two additional parameters to equation 1.

Results from this study suggest that this parasitoid could be effective in reducing populations of *C. ferrugineus* in grain bins. It was able to attack up to 7.5 larvae per 12-h period. This is a relatively high attack rate compared with other stored-grain parasitoids. *Choetospila elegans* (Westwood), a hymenopteran parasitoid of the lesser grain borer, *Rhyzopertha dominica* (F.), has a parasitization rate of about half that of *C. waterstoni* (unpublished data). *C. waterstoni* has been found throughout the grain mass in bins of stored wheat (Hagstrum 1987). Thus, it should be able to parasitize hosts that are located in any region of the grain mass. The parasitoid also attacked *C. ferrugineus* larvae over the full range of temperatures (25–35°C) that are optimal for its growth (Smith 1965).

There are two facets of parasitization that need to be considered in developing a model for this parasitoid: host finding and oviposition. This wasp can paralyze and feed upon hosts without oviposition, and they can paralyze many more hosts than

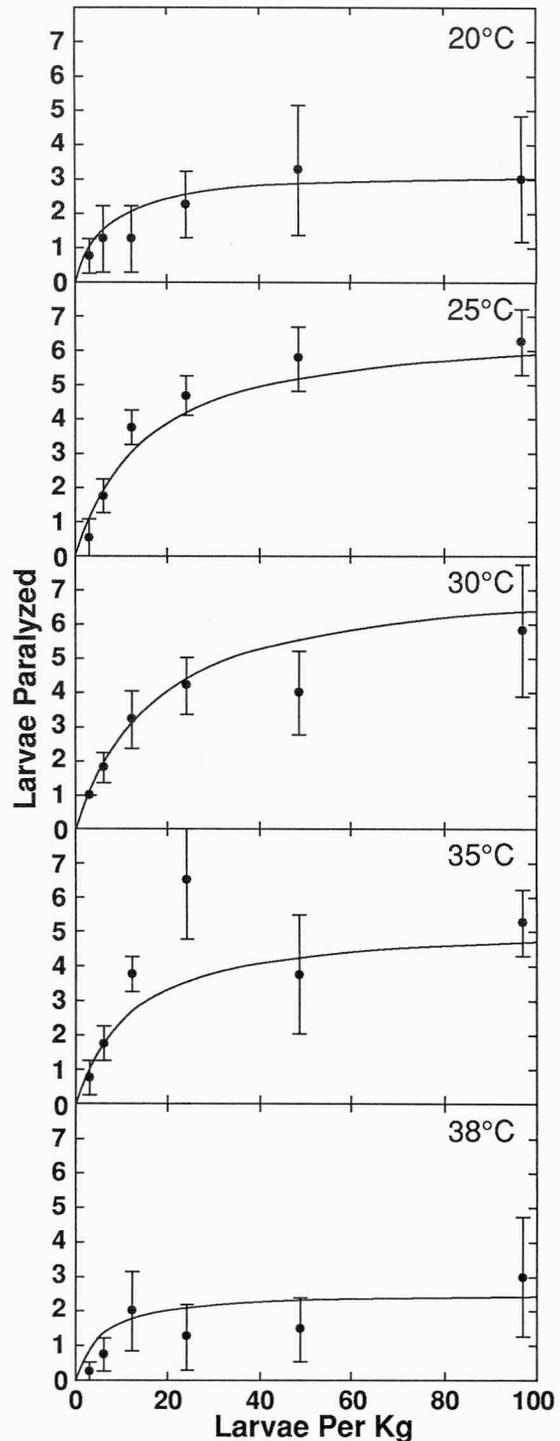


Fig. 1. Functional response of *C. waterstoni* paralyzing fourth-instar rusty grain beetle at five different temperatures. A type II functional response model that includes handling time as a function of temperature was fit to the entire data set using nonlinear least squares. Vertical bars indicate SE of the mean.

they can lay eggs on. Thus, oviposition rate is the limiting factor. If at least one host is found in a 24-h period, the parasite could lay its maximum of two or three eggs on it. The parasitism rate will not increase, even if more hosts are found. Host feeding is also an important mortality factor that would need to be included in a model for *C. waterstoni*. Yano (1989) found that including host feeding in his model stabilized the interactions of *Encarsia formosa* Gahan parasitizing the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood). Host feeding is a desirable character for biological control agents because it not only depresses host density but also has a stabilizing effect on the system (Yamamura & Yano 1988). Hosts that are paralyzed but are not killed by host feeding may provide additional stability to the system. In the case of *C. waterstoni*, paralyzed larvae do not progress to the next developmental stage; thus, they remain available for oviposition for at least 2 wk (Rilett 1949). This can result in a type of self-provisioning that may enable the wasp to survive periods of low host availability. A similar type of self-provisioning is exhibited by *Bracon hebetor* Say parasitizing *Ephestia cautella* (Walker) (Hagstrum 1983).

This parasitoid may be one of the best candidates for biological control of a stored grain beetle. Its chances of finding a suitable host may be much greater than for other stored grain parasitoids that only attack beetles developing inside the grain kernel. Howard & Flinn (1990) found that chemical cues are probably used by this parasitoid to locate potential hosts within a grain mass. The host larvae appear to leave a kairomonal trail as they move through the grain. If the wasp uses these trails to locate hosts or host aggregations within the grain mass, it may also tend to aggregate in patches of high host density (Howard & Flinn 1990). In addition, *C. waterstoni* further increases host mortality by attacking and feeding on all instars. Its generation time is half that of its host (unpublished data), and it is very host-specific. Searching efficiency is usually higher in host-specific parasitoids (Hassell 1978) and can lead to a greater depression of host equilibrium.

Information from this study will be used to develop a parasitoid model that will be coupled to a simulation model for *C. ferrugineus* (Hagstrum & Flinn 1990). This model should greatly increase our understanding of this parasitoid's effect on *C. ferrugineus* populations and can be used to design an efficient biological control program.

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