

Simulation Model of *Cephalonomia waterstoni* (Hymenoptera: Bethyridae) Parasitizing the Rusty Grain Beetle (Coleoptera: Cucujidae)

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ABSTRACT We have developed a simulation model of parasitic grain wasp, *Cephalonomia waterstoni* (Gahan), parasitizing the rusty grain beetle, *Cryptolestes ferrugineus* (Stephens). The model predicts host and parasitoid phenology based on grain temperature, using a distributed-delay method to simulate variance in developmental rate. The model accurately predicted both the time and magnitude of peak parasitoid density. Changing the timing of parasitoid release had a greater effect than releasing more parasitoids. Releasing parasitoids at day 20 instead of day 40 reduced the maximum host population by 75%. Parasitoids are most effective when releases are timed so that parasitoids find the 1st-produced 4th-instar. This model should be a valuable tool for developing a biological control program for *C. ferrugineus* on stored wheat. It can be used to predict the optimum time of release, the number of parasitoids to release, and the effects of other controls such as fall aeration.

KEY WORDS parasitoid, model, stored-product, biological control

PARASITOID AUGMENTATION IS most successful when the proper number of parasitoids are released at the correct time. Models of insect parasitoids and pests can provide insight into when and how many parasitoids should be released (Kareiva 1990). The idea of using parasitoids or predators for control of stored grain has been around for a long time (Brower 1990). However, it was not until recently that the Federal Register (Anonymous 1991) published a proposed regulation that would allow the release of parasitoids and predators into stored grain.

The rusty grain beetle, *Cryptolestes ferrugineus* (Stephens), is one of the most abundant pests of farm-stored wheat in the United States. Adults and larvae feed primarily on the wheat germ and can cause considerable damage. Parasitic grain wasp, *Cephalonomia waterstoni* (Gahan), is a hymenopteran parasitoid of the rusty grain beetle, and is frequently found in stored grain (Sinha et al. 1979). This parasitoid may often prevent rusty grain beetle populations from reaching damaging levels (Hagstrum 1987), and is potentially useful as a biological control agent. Although this wasp will parasitize larvae of other *Cryptolestes* species, when given a choice, it prefers *C. ferrugineus* (Finlayson 1950). This wasp usually oviposits on 4th instars exclusively; however, it will paralyze and feed on 1st-3rd instars (Rilett 1949). Earlier instars frequently feed within the wheat germ (Rilett 1949), where they

are less likely to be attacked. In contrast, 4th 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, paralysis occurs within 1 min. The wasp will paralyze more hosts than it can oviposit on, and the paralyzed larvae do not recover. The wasp usually lays 1-2 eggs per host. It has a relatively low fecundity, laying on average 2.3 eggs per day (Finlayson 1950). Wasp larvae feed externally on the host and mature rapidly. The generation time of the wasp is ≈ 14 d at 30°C. The adults live for ≈ 15 d. There are no age-structured host-parasitoid models for stored-product insects. This type of model is necessary to accurately simulate overlapping generations that commonly occur in stored grain.

In this article, we develop a distributed delay model of *C. waterstoni* and couple it to an existing model of *C. ferrugineus*. This model increases our understanding of parasitoid effect on *C. ferrugineus* populations and can be used to design an efficient biological control program.

Materials and Methods

Developmental Rate and Survivorship. Temperature-dependent developmental rate and survivorship of *C. waterstoni* eggs, larvae, and pupae were estimated at 6 different temperatures. Wasps and beetles were obtained from a

culture maintained at the U.S. Grain Marketing Research Laboratory. Field-collected adults were added to the cultures each year to maintain genetic diversity. Individual, mated 3-d-old *C. waterstoni* females and 4th instar *C. ferrugineus* larvae were placed into glass vials (13 by 44 mm). Filter paper was secured to the top of the vial with screw-on septum tops. Each wasp was removed from the vial after stinging and ovipositing on a host larva. Vials containing individual parasitized larvae were put into unlit environmental chambers, which were maintained at temperatures of 20, 25, 30, 35, 38, and $40 \pm 1^\circ\text{C}$ and $75 \pm 5\%$ RH. At least 40 eggs were observed at each temperature. Larvae were checked daily for development. Because it is extremely difficult to discern instars without harming parasitoid larvae, we recorded only the time from egg hatch to beginning of pupation, and from pupae to adult emergence. A nonlinear 4-parameter developmental time equation with high temperature inhibition (Wagner et al. 1984) was fit to the data:

$$D_t = \frac{1 + \exp\left[\frac{HH}{1.987}\left(\frac{1}{TH} - \frac{1}{T}\right)\right]}{RHO25 \frac{T}{298.15} \exp\left[\frac{HA}{1.987}\left(\frac{1}{298.15} - \frac{1}{T}\right)\right]} \quad (1)$$

where D_t is developmental time, T is Kelvin temperature, $RHO25$, HA , HH , and TH are fitted parameters. The model was fit to developmental time instead of rate because of potential problems with least-squares estimates of developmental rate (Kramer et al. 1991).

A discrete, distributed-delay model (Manetsch 1976) written in Pascal was used to predict population growth of the parasitoid *C. waterstoni* as a function of grain temperature. The insect model consists of the following 4 major parts: (1) an equation describing the relationship between the daily rate of immature insect development and grain temperature, (2) a delay process for moving the immature insects through the stages and simulating variation in developmental time, (3) a temperature-dependent delay process that simulates ageing of adult male and female wasps, and (4) an equation that predicts female fecundity as a function of age and grain temperature. The Manetsch model uses an Erlang density function to describe the shape of the curve of the individuals leaving a stage over time. The k values for the Erlang function were calculated as (mean developmental time)²/variance.

Functional Response. We used a temperature dependent functional response model (Flinn 1991) to couple the parasitoid model with the host model. This equation was modified from Royama (1971) to include the effects of host density and temperature on host attack rate:

$$N_a = N_t \left[1 - \exp \left\{ - \frac{a \cdot H \cdot P_t}{1 + a \cdot (B_0 - B_1 \cdot T + B_2 \cdot T^2) \cdot N_t} \right\} \right] \quad (2)$$

where N_a is the number of 4th instar hosts per kilogram that are paralyzed, N_t is the number of 4th instar hosts per kilogram that are available, a is the instantaneous search rate (0.04797), H is time (24 h), B_0 is 19.918, B_1 is 11.289, B_2 is 0.02266, P_t is the number of adult female parasitoids per kilogram, and T is the Celsius grain temperature.

Coupling Models. The *C. waterstoni* model was coupled to a modified version of the rusty grain beetle model (Hagstrum and Flinn 1990) (Fig. 1). Both the beetle and wasp models use a daily time step. This wasp can paralyze and feed on hosts without oviposition, and it can paralyze many more hosts than it can lay eggs on. If at least 1 host is found in a 24-h period, then the parasitoid can lay her daily maximum of 2–6 eggs (Rilett 1949). The parasitism rate will not increase even if more hosts are found. In the model, the number of 4th-instar beetles is reduced by the number that are paralyzed, which is determined by the functional equation. We modeled parasitoid oviposition using an if-then-else statement: if the number of female wasps is greater than the number of paralyzed 4th instars, then the number of new eggs laid is equal to the number of paralyzed 4th instars (parasitization is limited by the number of paralyzed 4th instars). Otherwise, the number of new eggs laid is equal to the number of female wasps in the age group times the age specific fecundity for that age group. After the final pupal stage in the model, the number of new adult female and male wasps is 2:1 based on a female to male sex ratios estimated by Rilett (1949) and Finlayson (1950).

Model Testing. Experiments were conducted in six 24.7-liter cylindrical plastic pails (38 cm tall by 31 cm diameter) that contained 19.4 kg of hard red winter wheat at 13% moisture. Containers were placed in an unlit environmental chamber maintained at $29.5 \pm 1^\circ\text{C}$ and $75 \pm 5\%$ RH. Ten adult male and 10 adult female *C. ferrugineus* were added to each container. These beetles were obtained from a laboratory culture and were 3–6 d old. Twenty days later, 2 adult male and 2 adult female *C. waterstoni* were added to each of 3 containers. The wasps were obtained from a laboratory culture and were ≈ 2 d old. The containers were covered with 122-mesh polyester silk-screen (Majestic Arts, Somers, NY) to prevent insects from entering or leaving the containers. The grain was sampled every 2 wk with a miniature compartmented grain trier (Fig. 2), taking 9 trier samples per container (Fig. 3). The grain from each trier sample weighed ≈ 29 g. Adult and immature stages

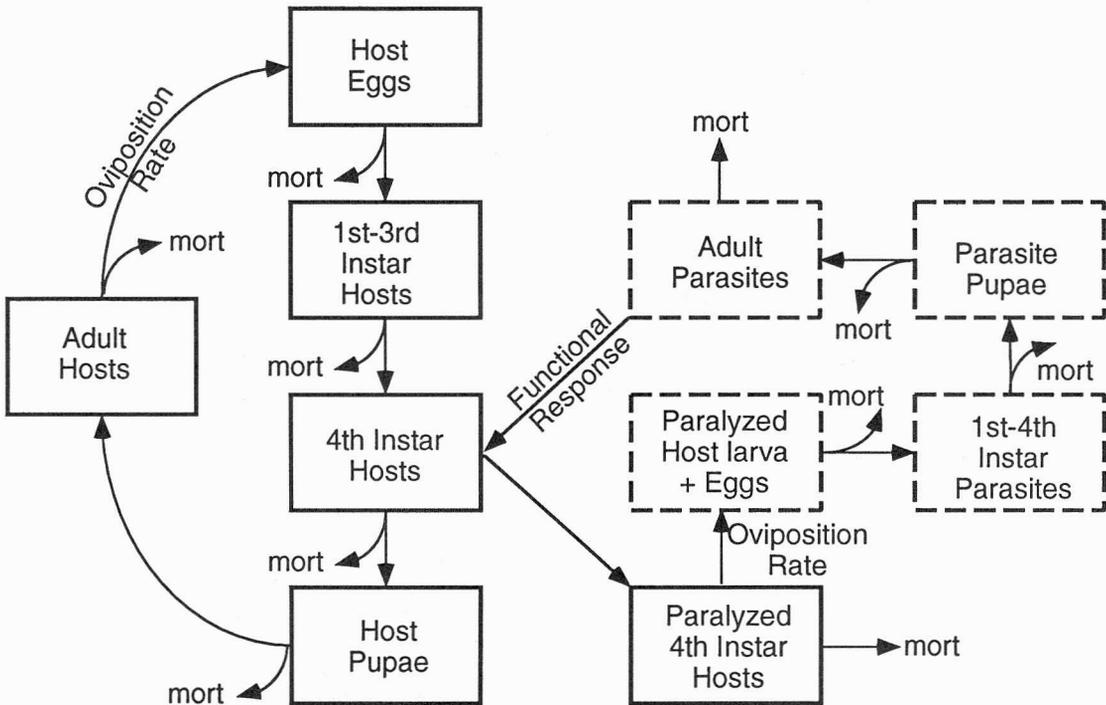


Fig. 1. Flow diagram of parasitoid and host models.

were counted. However, only adults were compared, because of difficulties of accurately sampling the immature stages that develop in the wheat germ.

Means and standard errors for *C. waterstoni* development time, nonlinear model for developmental time, and predicted versus measured insect densities were estimated using the statistics, nonlinear and regression analysis procedures of SYSTAT version 5.2 (Wilkinson et al. 1992).

Results

Immature Developmental Time and Survivorship. *C. waterstoni* had the highest survivorship at 30°C (98.5%) (Table 1). No eggs or larvae survived at 40°C. At 20 and 38°C, most of the mortality occurred during eclosion; the wings of newly emerged adults often failed to expand fully and the adults were dried up in appearance. Development was shortest at 35°C and the longest at 20°C ranging from 9 to 47 d. The Wagner 4-parameter developmental time equation with high temperature inhibition (Wagner et al. 1984) fit the data very well for both the egg-larval stages and the pupal stage (Table 2).

Adult Longevity. Adult longevity was temperature dependent, and adults lived much longer at cooler than at warmer temperatures (Fig. 4). The \log_e mean adult longevity in days was regressed against \log_e of temperature for females $\log_e(\text{days}) = 13.27 - 2.95 * \log_e(\text{temperature})$ $r^2 = 0.99$, $N = 5$, $P = 0.0004$, and for males $\log_e(\text{days}) = 10.02 - 2.35 * \log_e(\text{temperature})$ $r^2 = 0.95$, $N = 5$, $P = 0.0055$). A distributed delay model using a discrete delay was used to model adult female and male

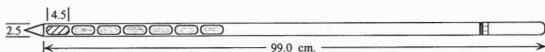


Fig. 2. Diagram of miniature compartmented grain trier.

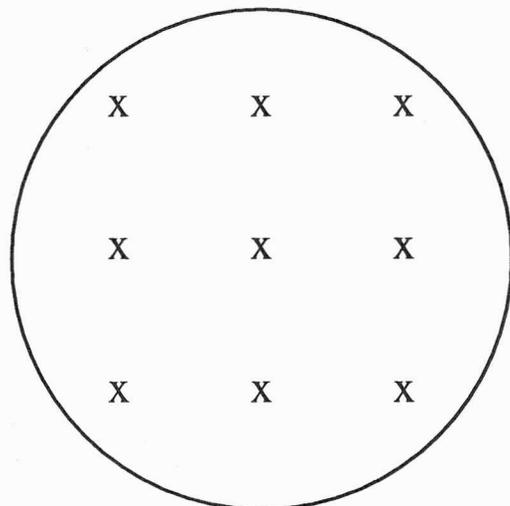


Fig. 3. Sampling locations in the containers.

Table 1. Percentage of survivorship and mean developmental time in days for immature *C. waterstoni* as a function of temperature

Temp, °C	Egg to pupa ± SEM	Survivorship	Pupa ± SEM	Survivorship	N
20	23.78 ± 0.50	72.5	23.54 ± 0.63	25.0	51
25	11.58 ± 0.42	94.2	10.83 ± 0.39	97.9	52
30	5.50 ± 0.15	98.5	7.28 ± 0.13	97.1	69
35	4.00 ± 0.01	95.8	4.82 ± 0.12	89.1	48
38	4.80 ± 0.12	80.0	5.08 ± 0.24	50.0	40

Relative humidity was 75 ± 5%, no immatures survived at 40°C.

longevity. The mean delay was based on the above regression equations, and *k* values of 50 and 25 were used for the female and male adults, respectively. The *k* values for the Erlang function were based on the mean developmental time²/variance.

Age-Specific Fecundity. When hosts are not limiting, the maximum number of eggs laid by a given female was based on her age and temperature. No eggs were laid at 40°C, and almost none were laid at 20°C. Five-day-old females had the highest rate of oviposition at 35°C. Age specific fecundity per day was modeled using the equation:

$$Z = -C_0 \cdot (Y - 20) \cdot (Y - 40) \cdot Y \cdot X^{-(C_1 + C_2 \cdot Y - C_3 \cdot Y^2)} \cdot e^{-(Y-20) \cdot C_4 \cdot X} \quad (3)$$

where *Z* is eggs per female per day, *Y* is temperature, *X* is female age in days. This equation was selected on a purely mathematical basis for its ability to fit a complex surface. A nonlinear statistical program was used to estimate the coefficients *C*₀, *C*₁, *C*₂, *C*₃, and *C*₄ whose values were 0.00049, 3.42234, 0.22571, 0.00233, and 0.01625, respectively. The equation fit the data well (*r*² = 0.90, *N* = 133, *P* < 0.0000001). The *Y* = 20 and *Y* = 40 parameters were used to constrain fecundity to zero when temperature was ≤20 or ≥40°C. Fig. 5 shows the mean age-specific fecundity at 25, 30, 35°C, and the predicted values using equation 3, and thus, are not shown. The 20 and 40°C graphs are not shown because age-specific fecundity was zero at 40°C and very low at 20°C. Age-specific fecundity was highest at 35°C and lowest at 20 and 40°C. At 25°C, eggs continued to be laid up to age 55. However, the rate of egg laying at 25°C was ≈1/2 compared with 30 or 35°C.

Model Testing. A comparison of observed versus predicted densities showed that, in the 3 containers without parasitoids, the model accurately predicted adult beetle density, except for the last

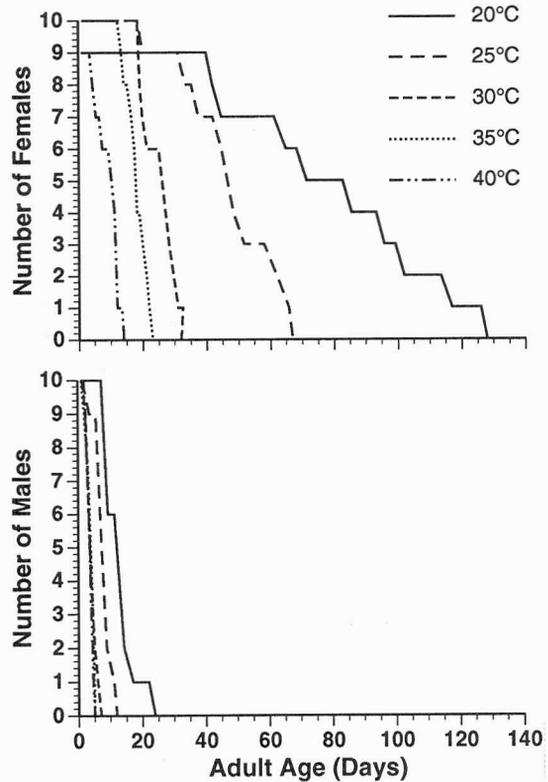


Fig. 4. Longevity of *C. waterstoni* adults as a function of grain temperature.

sample date (Fig. 6). After 175 d, adult beetle population reached an average density of 2,693/kg. In containers with both beetles and parasitoids, the model predicted the 1st peak wasp density earlier than the actual 1st peak (Fig. 7). However, the 2nd peak wasp density was predicted very accurately by the model. The model estimate of 1st peak beetle density was very close to the actual 1st peak beetle density. The model predicted the onset of the 2nd beetle population peak ≈ 10 d earlier than when the actual peak occurred. Predicted versus actual host and parasitoid densities were compared using regression analysis (Table 3). The slopes and intercepts were not significantly different (*P* < 0.05, *N* = 10) from 0 and 1, respectively, for containers with both parasitoids and beetles, or with beetles alone (a slope of 1 and an intercept of 0 indicates good agreement). The *r*² values ranged from 0.80 to 0.99.

Table 2. Parameter estimates for the Wagner 4 parameter developmental rate equation with high temperature inhibition, for *C. waterstoni*

Life stage	RH025 ± ASE	HA ± ASE	HH ± ASE	TH ± ASE	R ²	N
Egg-larval	0.0887 ± 0.0022	25,427.8 ± 919.8	89,028.4 ± 22,851.8	310.02 ± 0.54	0.99	80
Pupal	0.3876 ± 0.0688	55,700.7 ± 4,950.6	48,203.0 ± 4,985.9	293.92 ± 0.60	0.99	81

ASE, asymptotic standard error.

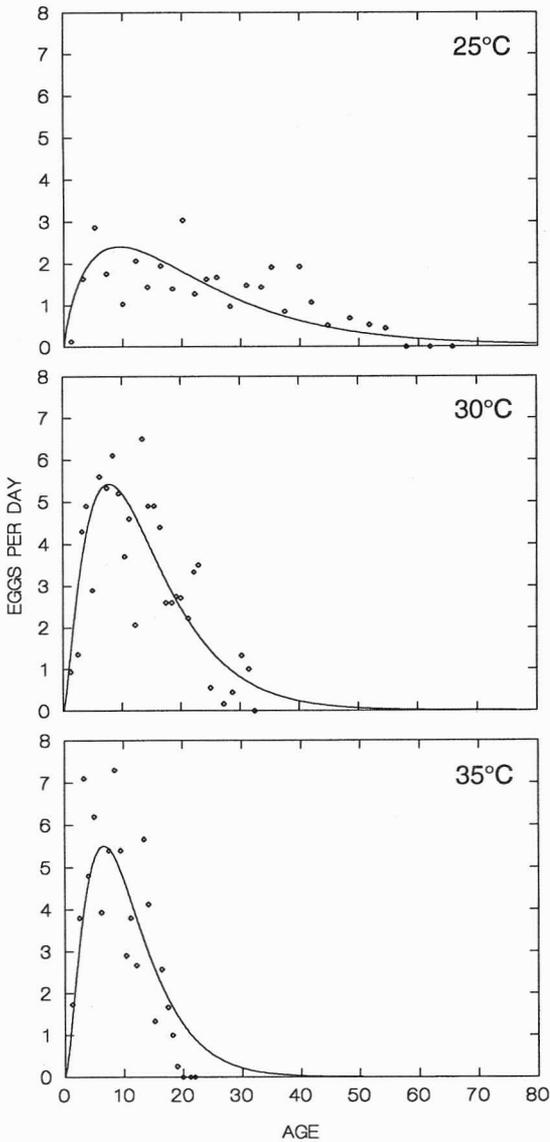


Fig. 5. Mean age-specific fecundity of *C. waterstoni* at 25, 30, 35°C, and predicted values using equation 3.

Cephalonomia waterstoni suppressed *C. ferrugineus* populations quite well. After 170 d, the average host density in containers with parasitoids was 146 beetles per kilogram. In containers without parasitoids, the average density was 2,693 beetles per kilogram. Thus, the parasitoids suppressed adult host populations by 95% compared with containers without parasitoids. The wasp generation time is ≈ 13 d at 29.5°C, so the parasitoids would go through ≈ 2.5 generations for each beetle generation. In the control, adult beetles increased rapidly after 100 d. In the containers with wasps, the beetle population started to increase rapidly after 130 d, then started to decrease after 160 d. The time between cycles was ≈ 70 d for both parasitoids

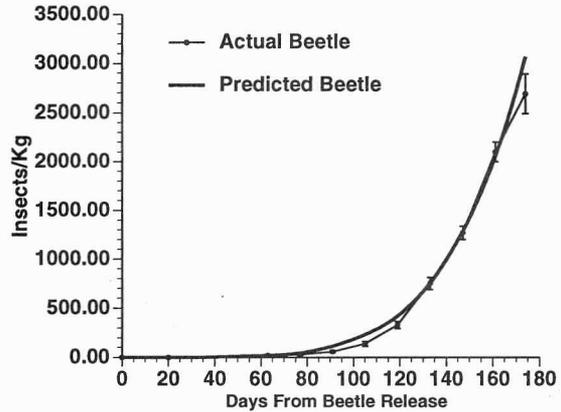


Fig. 6. Mean observed and predicted *C. ferrugineus* densities in 3 cylindrical plastic pails (24.7 liter) that contained 19.4 kg of hard red winter wheat at 13% moisture and 29.5°C. Containers were placed in an unlit environmental chamber maintained at $29.5 \pm 1^\circ\text{C}$ and $75 \pm 5\%$ RH. Five pairs of adult *C. ferrugineus* were added to each container. Vertical bars indicate standard errors.

and beetles. Seventy days is ≈ 2 times the beetle generation time. Although the wasps were introduced 20 d after the beetle release, some of the 2nd generation beetles managed to escape from parasitization. The fact that the beetle population increased rapidly after 130 d suggests that many of the beetle 4th instars and pupae were able to escape parasitization when the parasitoid density was low (day 110–135) (Fig. 7).

Model Simulations. In simulations with the model, changing the timing of parasitoid release had a greater effect on host density than releasing more parasitoids (Fig. 8 A and B). Releasing parasitoids at day 20 instead of day 40 reduced the maximum host population by 77% (19/kg versus 85/kg). Fig. 8C shows that 20 times as many parasitoids needed to be released after 40 d to get the same level of suppression as releasing 2 pairs of parasitoids after 20 d.

Discussion

There were 2 major population peaks in both the host and wasp populations during the 175-d experimental period. The 2nd peak was much higher than the 1st peak for both species (Fig. 7). The model predicted the magnitude of the 2nd host peak relatively accurately. This suggests that the model is correctly estimating the number of beetle larvae that are escaping parasitization during the 1st generation. However, the model did predict the 2nd host peak ≈ 10 d earlier than it should have. This may have been the result of a slight overestimation of the rate of nonparasitized host development. The timing of the 2nd wasp peak was very accurate. As with any model, the longer we want to predict into the future, the more difficult it is to predict an event accurately. The

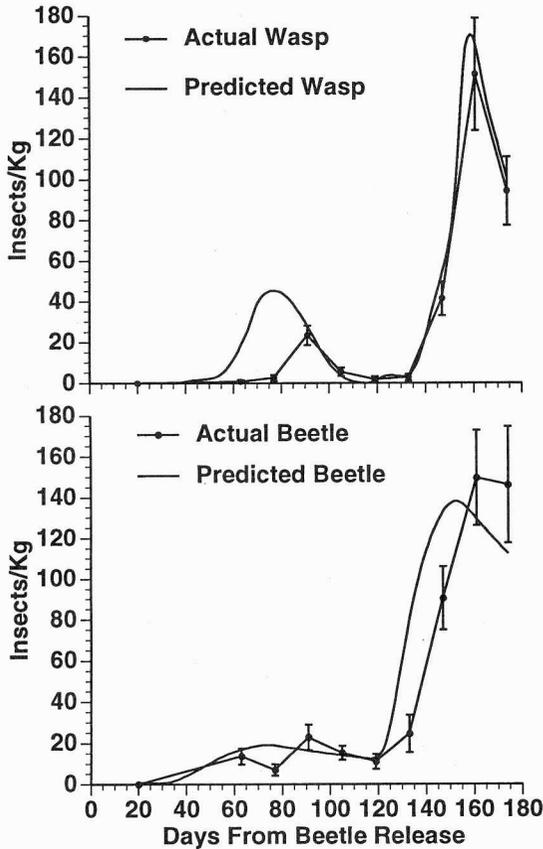


Fig. 7. Mean observed and predicted *C. waterstoni* and *C. ferrugineus* densities in 3, cylindrical plastic pails (24.7 liter) that contained 19.4 kg of hard red winter wheat at 13% moisture and 29.5°C. Containers were placed in an unlit environmental chamber maintained at 29.5 ± 1°C and 75 ± 5% RH. Five pairs of adult *C. ferrugineus* were added to each container, 20 d later, 2 pairs of adult *C. waterstoni* were added to each container. Vertical bars indicate standard errors.

fact that this model was able to predict the population dynamics well for 175 d suggests that it may prove to be a useable model for stored wheat. Typically, wheat is stored for up to 150 d before grain temperatures fall below 20°C in the winter. Once the grain temperature falls below 20°C, neither the host or wasp population will develop significantly.

The model did tend to overestimate the effectiveness of the parasitoids to reduce the host population. This suggests that the functional response equation is overestimating the attack rate. Previous functional response experiments (Flinn 1991) were conducted with only 4th instars available. Because these wasps locate 4th instars by trail following (Howard and Flinn 1990), the presence of other host stages could make trail following of 4th instars more difficult. Another possibility is that when host density is high, female wasps spend most of their time stinging hosts rather than ovipositing. Be-

Table 3. Regressions of actual versus predicted parasitoid density, and actual versus predicted beetle density (with and without the parasitoid), N = 10

	Slope	SEM	Intercept	SEM	r ²
Beetle	0.96	0.17	-3.46	12.80	0.80
Parasitoid	0.92	0.08	-6.42	5.57	0.94
Beetle (alone)	0.93	0.03	-5.26	35.66	0.99

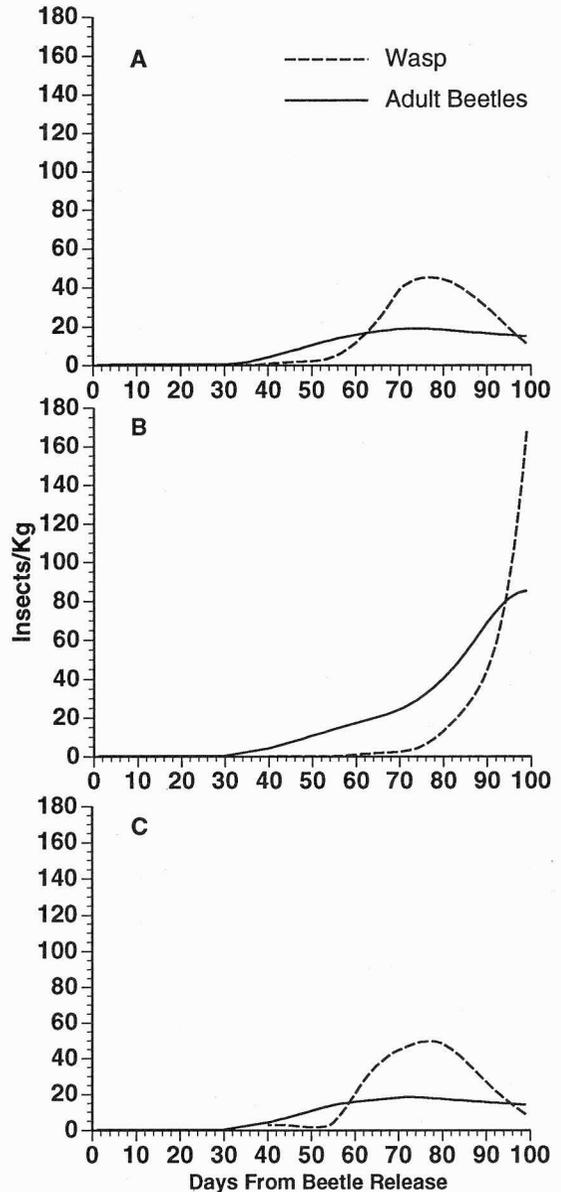


Fig. 8. Model predictions of *C. ferrugineus* and *C. waterstoni* population dynamics. Starting conditions for A, B, C were 5 pairs of adult *C. ferrugineus* in 19.4 kg of hard red winter wheat at 13% moisture and 29.5°C. Two pairs of parasitoids released 20 d after host release. Two pairs of parasitoids released 40 d after host release. Forty pairs of parasitoids released after 40 d.

cause wasp eggs often become detached from larvae when sampling the grain, I was only able to measure the number of paralyzed hosts in an earlier functional response experiment (Flinn 1991).

In model simulations, changing the timing of parasitoid release had a greater effect than releasing more parasitoids. Optimal timing of parasitoid release depends on parasitoids finding the 1st-produced 4th-instar beetles. The most effective control will be obtained when parasitoids are released in time to attack new 4th-instars. Sufficient numbers need to be released to attack most of the 4th-instar beetles before they can become adults. Simulations with the model indicated that releasing a wasp density that is equal to the parental host density should result in sufficient host population reduction. Based on field data (Hagstrum 1987), we estimate that the immigration rate for *C. ferrugineus* is ≈ 10 beetles per 27 ton/d (1,000 bu/d). If we assume that ≈ 200 *C. ferrugineus* immigrate into an 81-ton (3,000-bu) bin during the 1st wk, then good control should be obtained by releasing 200–400 parasitoids 20 d after the grain was stored.

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 that develop inside the grain kernel. Howard and 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 kairomone 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 and Flinn 1990). In addition, *C. waterstoni* further increases host mortality by attacking and feeding on all instars (Finlayson 1950). Its generation time is half that of its host, 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.

This model should be a valuable tool for developing a biological control program for *C. ferrugineus* on stored wheat. It can be used to predict both the optimum time of release and number of parasitoids to release. The addition of the parasitoid model should make model predictions of *C. ferrugineus* more realistic when this parasitoid is present in the grain. This model will be incorporated into an existing expert system for stored grain management (Flinn and Hagstrum 1990). This will allow the system to make more accurate recommendations for a particular storage situation.

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