Monitoring and Predicting Population Growth of *Rhyzopertha dominica* (Coleoptera: Bostrichidae) Over a Range of Environmental Conditions

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ABSTRACT Population growth of lesser grain borer, *Rhyzopertha dominica* (F.), in 135-kg lots of hard red winter wheat, *Triticum aestivum* L., was monitored at 3 grain moisture levels (≈10, 12, and 14%) at each of 3 temperatures (≈22, 27, and 32°C). Over this range of environmental conditions, a published population growth model explained 64–96% of the variation in insect density. Based on published studies and new data collected for developmental times, new equations were developed for egg production and developmental time, and daily adult mortality was estimated. Substituting new equations and mortality rate in the published model improved predictions, increasing by 3–24% the percentage of variation explained. The biggest improvements tended to be at the extreme grain moisture and temperature conditions.

KEY WORDS *Rhyzopertha dominica*, stored products, developmental time, computer simulation model, grain moisture, temperature

VALIDATION OF MODELS for insect population growth with field-collected data is difficult because it is hard to control or measure all of the factors that affect population growth, such as insect parasitoids or changes in grain moistures and temperatures. With farm-stored grain, the number of insects initiating an infestation is difficult to measure, and farmers often sell grain or control insects before enough data have been collected for validating the model. High insect fecundity generally precludes monitoring population growth rates in small containers (<1 kg) in the laboratory to validate models because crowding reduces survival and egg production (Solomon 1953) and thus population growth rate (Birch 1953, Sidik 1982, Demianyk and Sinha 1987). Each of these population growth studies was done under only a single grain moisture and temperature condition. Artificially infesting 135-kg (5-bu) lots of wheat, *Triticum aestivum* L., in walk-in controlled environment chambers provides an alternative approach to studying the population dynamics of lesser grain borer, *Rhyzopertha dominica* (F.)(Hagstrum and Flinn 1990, 1994). This approach provides realistic results because *R. dominica* tends to aggregate in a small area in the top center of the grain mass similar in size to this 135-kg lot (Hagstrum 1995).

The primary purpose of the current study was to measure the growth of *R. dominica* populations at 9 combinations of grain moisture and temperature conditions. These data were used to check the predictions of a published computer simulation model (Hagstrum and Throne 1989) for *R. dominica* population growth and to explore the potential for improving model predictions by using new life history data.

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Materials and Methods

The growth rates of *R. dominica* populations were studied by infesting each of 27 lots of 135 kg (5 bu) of hard red winter wheat in 208-liter (55 gal) steel drums with 5 pairs of recently emerged adults. Three lots of wheat at each of 3 moisture contents (≈10, 12, and 14%) were held at each of 3 temperatures (≈22, 27, and 32°C) in walk-in chambers. Tops of the drums were covered with fine-mesh cloth for ventilation. Population estimates were made during the first 2 generations every week at 27–31.5°C and every 2 wk at 22–23°C by taking wheat samples with a grain trier (Model 39-A-OH, Seedburo Equipment, Chicago, IL) at 4 locations in each drum, 2 in the center and 2 halfway between the center and the edge of the drums. Each wheat sample was weighed, and insect densities were calculated as insects per 0.5 kg of wheat. On each sampling date, the moisture of each grain sample was determined with a moisture meter (Model GAC II, Dickey-John, Auburn, IL), and temperature was checked at sampling locations with a thermistor probe (Model 8523, Cole-Parmer Instrument, Chicago, IL).

To determine the developmental times of *R. dominica* at 22, 25, 27, 32, and 37°C, groups of several hundred adults were allowed to oviposit on 100-ml lots of 12% hard red winter wheat for 24 h. Beginning on days 68, 43, 33, 24, and 20 at 22, 25, 27, 32, and 37°C, respectively, the grain was x rayed every other day at 22°C and every day at 25, 27, 32, and 37°C to determine the number of insects molting from the pupal to the adult stage. An x ray unit (Grain Inspection Unit, General Electric, Milwaukee, WI) at 20 kv, 5 ma and x ray film (36 × 43 cm)(Industrex M, Kodak, Rochester, NY) were used. Exposure time was 1.5 min. The numbers of pupae and adults on each x-ray were counted using a dissecting microscope.

The distributed delay model of Hagstrum and Throne (1989) was used to simulate the population growth of *R. dominica*. The model consists of the following 4 major parts: (1) equations describing the relationship between insect developmental time and grain moisture and temperature; (2) a delay process for moving the immature insects through the stages and simulating variation in developmental time; (3) a 200-element array for keeping track of adult age; and (4) equations describing the relationship between grain moisture, temperature, and egg production. Mortality of immature and adult insects was generally considered to be 0, although the offspring production data used in the model include immature mortality. Also, daily adult mortality with the new model was 1% at 22–23°C, at 10.4% grain moisture and 27°C, and at 11.5% grain moisture and 27.5°C. The effects of grain moisture on developmental times were simulated by linear interpolation with a 1.3-fold increase in developmental times between 14 and 10% grain moisture.

The means and standard errors for insect densities, equations for egg production and developmental times, and the regression of measured against predicted insect densities were calculated using commercial statistical analysis software (SAS Institute 1990).

Results

A published model (Hagstrum and Throne 1989) predicted no population growth by *R. dominica* populations at 22°C and 10% grain moisture content (Fig. 1A) so a regression equation could not be reported in Table 1; the published model also did not predict changes in population density at 31 or 31.5°C (r^2 = 0.64–0.72) as well as at other conditions (r^2 = 0.79–0.96) (Fig. 1; Table 1). Except at 22.5 and 12% moisture content, the slopes for regression of measured versus predicted densities were not significantly different from 1, indicating that the model provided fairly good predictions of insect population growth, and none of the intercepts was significantly different from 0. However, the tendency for 5 of 7 slopes to exceed 1.2 with the published model is the result of daily egg production being underestimated and the predicted developmental times being too long. Also, some adult mortality not included in the published model might be expected at low temperatures and moistures.

New equations were developed for daily egg production (Fig. 2) based on data from Beckett et al. (1994) and for developmental time (Fig. 3) based on new data (Table 2). The new equation for egg production (Y) as a function of temperature (T) and grain moisture content (M) was

$$Y = 0.296\,T - 0.0108\,T^2 + 2.302\,M - 0.118\,M^2 + 0.0306\,TM - 18.673 \quad (1)$$

with total df = 41, an r^2 of 0.895, and an MSE of 0.05077. The standard errors were 0.122, 0.00164, 0.824, 0.0348, 0.00589, and 5.256 for the parameters T, T^2, M, M^2, TM, and intercept, respectively. The new developmental time data was fit to the equation from Wagner et al. (1984) as

$$\text{Developmental time} = \frac{1 + \exp\left[\dfrac{HH}{1.987}\left(\dfrac{1}{TH} - \dfrac{1}{T}\right)\right]}{RHO25\,\dfrac{T}{298.15}\,\exp\left[\dfrac{HA}{1.987}\left(\dfrac{1}{298.15} - \dfrac{1}{T}\right)\right]} \quad (2)$$

where $RHO25$ = 0.0223, HA = 34,197.92, HH = 44,424.50, TH = 304.29, and T is Kelvin temperature with total df = 4, an $r2$ of 0.998, and a mean standard error of 6.8846. The standard errors were 0.00877, 11,333.87, 11,791.15, and 7.00 for the fitted parameters $RHO25$, HA, HH, and TH, respectively. Based on a study of *R. dominica* survival at low temperatures (Hagstrum and Flinn 1994), daily adult mortality rates were assumed to be 1% at 22–23°C, at 27°C and 10.4% moisture, and at 27.5°C and 11.5% moisture.

The new egg production and developmental time equations and adult mortality estimate generally improved model predictions (Fig. 1; Table 1), increasing $r2$ by 0.03–0.24. Also, 6 of 8 of the slopes were closer to 1 than with the published model, and all of the slopes had smaller standard errors.

The model was extremely sensitive to daily adult mortality rates (Fig. 4). At 27°C and 10.4% moisture, increasing or decreasing the 1% mortality rate by 1% resulted in a 59% increase or a 33% decrease, respectively, in the predicted *R. dominica* population densities at 91 d.

The points in Fig. 1 at which the predicted insect density begins to increase represents the emergence of the 1st offspring of the original females and, thus, the egg-to-adult developmental time at different combinations of grain moisture and temperature conditions. As adults emerge, the slope closely approximates the egg production per 0.5 kg of wheat per day. Developmental time was decreased by an average of 0.49–0.90 times and egg production increased by 1.47–2.99 times by a 5°C increase in temperature or a 2% increase in grain moisture (Table 3).

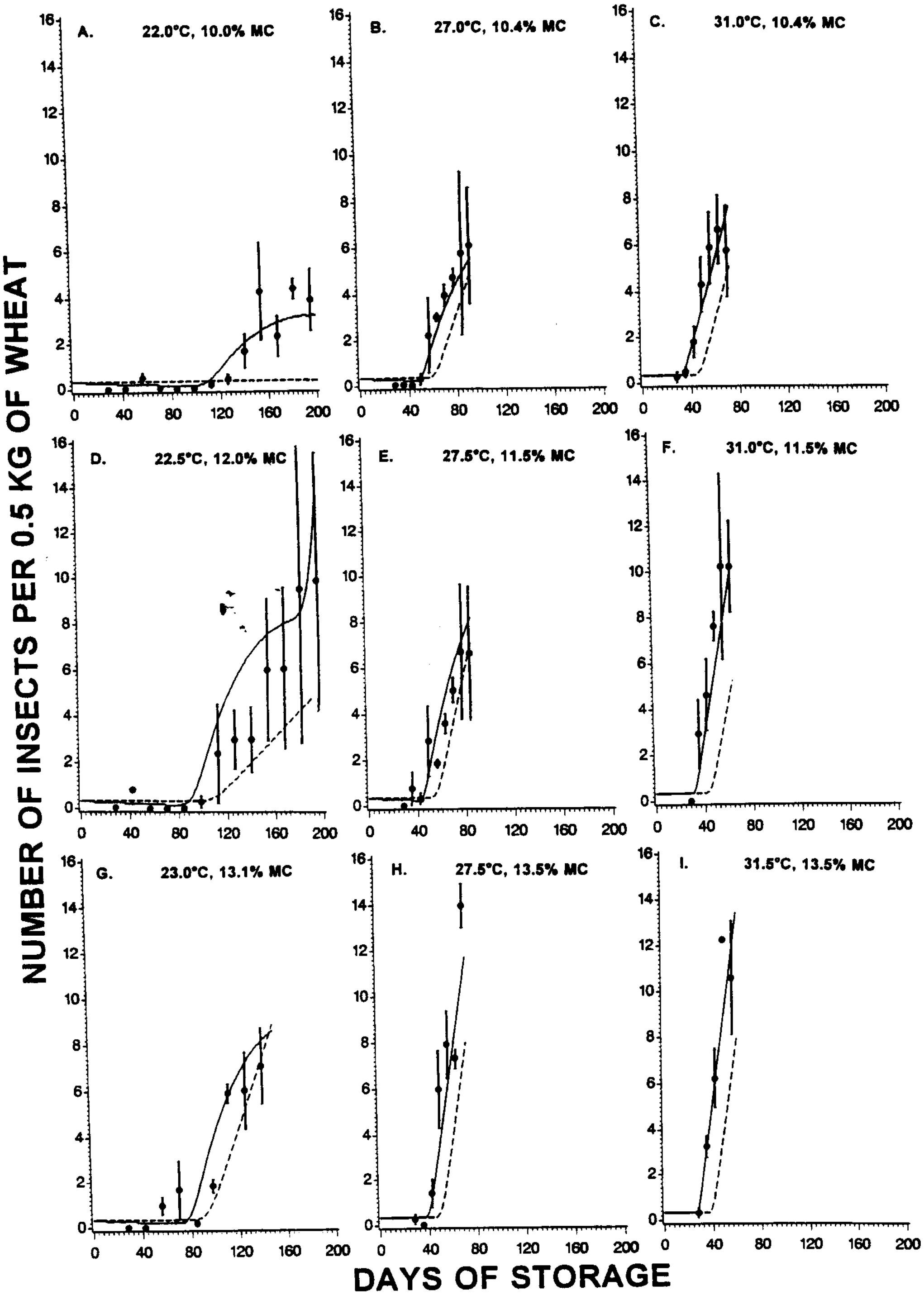

Fig. 1. Measured (dots) and predicted (lines) insect population densities in 135-kg lots of wheat infested with 5 pairs of *R. dominica* and held at 9 combinations of grain moisture content (MC) and temperature conditions (A-I). The vertical bars are standard errors for 3 replicates. Predictions were made with a published model (Hagstrum and Throne 1989) modified only to allow adults to live 200 instead of 70 d (dashed lines) or with a newly described model (solid lines).

Table 1. Parameters for regression of measured (y) against predicted (x) densities of *R. dominica* populations

Temp, °C	% moisture content	n	Slope (b_1) $b_1 \pm$ SE	Slope t	Slope P	Intercept (b_0) $b_0 \pm$ SE	Intercept t	Intercept P	r^2
					Published model				
22.5	12.0	13	2.14 ± 0.13	8.75	<0.001	−0.32 ± 0.30	−1.10	0.30	0.96
23.0	13.1	9	1.02 ± 0.15	0.20	0.85	0.51 ± 0.48	1.07	0.32	0.87
27.0	10.4	10	1.32 ± 0.22	1.48	0.17	0.57 ± 0.48	1.18	0.27	0.82
27.5	11.5	9	0.96 ± 0.15	0.25	0.81	0.93 ± 0.47	1.97	0.09	0.86
27.5	13.5	7	1.64 ± 0.37	1.72	0.14	1.50 ± 1.28	1.18	0.29	0.79
31.0	10.4	7	1.23 ± 0.41	0.57	0.59	1.50 ± 0.97	1.55	0.18	0.64
31.0	11.5	6	1.80 ± 0.56	1.43	0.21	2.71 ± 1.41	1.91	0.13	0.72
31.5	13.5	5	1.57 ± 0.58	0.99	0.38	2.68 ± 1.99	1.35	0.27	0.71
					New model				
22.0	10.0	12	1.19 ± 0.14	1.35	0.20	−0.29 ± 0.24	−1.23	0.25	0.88
22.5	12.0	13	0.77 ± 0.08	2.87	0.01	−0.19 ± 0.49	−0.38	0.71	0.89
23.0	13.1	9	0.83 ± 0.11	1.62	0.14	0.12 ± 0.45	0.27	0.80	0.90
27.0	10.4	10	1.17 ± 0.05	3.42	0.01	−0.05 ± 0.15	−0.33	0.75	0.99
27.5	11.5	9	0.80 ± 0.09	2.30	0.05	0.26 ± 0.39	0.66	0.53	0.93
27.5	13.5	7	1.15 ± 0.15	0.97	0.37	0.25 ± 0.90	0.28	0.79	0.92
31.0	10.4	7	0.96 ± 0.16	0.26	0.81	0.29 ± 0.68	0.43	0.69	0.88
31.0	11.5	6	1.07 ± 0.14	0.51	0.63	0.86 ± 0.79	1.08	0.34	0.94
31.5	13.5	5	1.05 ± 0.22	0.21	0.84	0.14 ± 1.60	0.09	0.94	0.88

The parameters and associated statistics are for regression models of the form $y = b_0 + b_1x$. When the intercept of the measured against predicted regression equation is not significantly different from 0, a slope of 1 indicates good agreement between measured (y) and predicted (x) insect population growth. Statistical significance of differences of intercepts from 0 and slopes from 1 were determined using t-tests.

Discussion

Population growth models can provide information about stored-grain insect populations that is needed to make pest management decisions (Hagstrum 1994). Forecasting population growth is important in determining when pest management will be needed. Population growth models also can be used to examine the effectiveness of a number of pest management programs so that a manager can select the most effective one (Flinn and Hagstrum 1990, Hagstrum and Flinn 1990). The reliability of a model as a pest management tool is determined by comparison of its predictions with the actual insect population growth rates.

The previous validation of the published model for *R. dominica* population growth over a narrow range of environmental conditions found that predictions explained 93% of seasonal variation in insect density (Hagstrum and Throne 1989). Over a wider range of environmental conditions in the current study, the r^2 ranged from 0.64 to 0.96 for the published model (Table 1). When the intercept of the measured against predicted regression equation is not significantly different from 0 as in the current study, a slope of 1 indicates good agree-

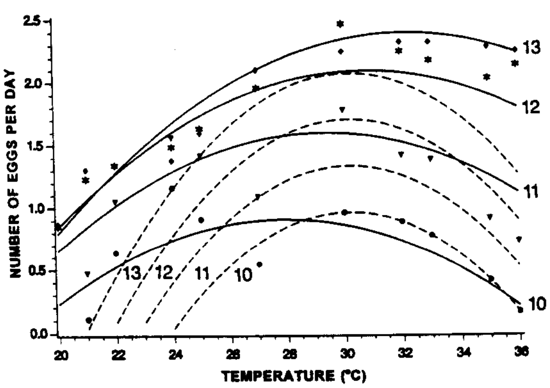

Fig. 2. Plots of the egg production equations used in published model (dashed line) and those based upon data of Beckett et al. (1994) (solid lines, equation 1). Egg production data of Beckett et al. (1994) were divided by 138 to give daily egg production per female similar to that predicted by equation used in published model at 27°C. Dots, triangles, asterisks, and diamonds represent data for 10, 11, 12, and 13% grain moisture, respectively, used to fit equation 1, and lines represent moisture levels indicated by numbers.

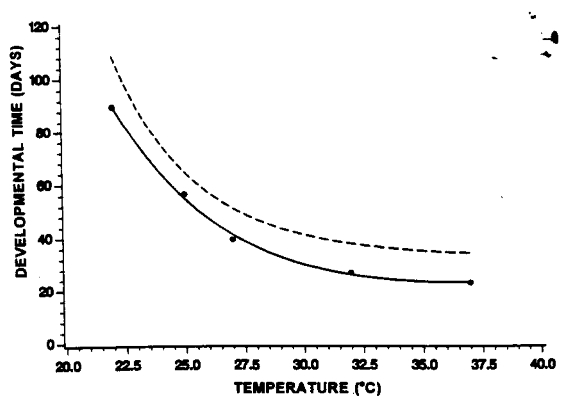

Fig. 3. Plots of the developmental time equations used in published model (dashed line) and those based upon current data (solid line, equation 2). Dots represent data in Table 2 used to fit equation 2.

Table 2. Developmental times of *R. dominica* on whole-kernel wheat, 12% moisture content, at 5 temperatures

Temp, °C	Developmental time, d		
	n	Mean	SD
22	275	89.8	9.41
25	613	56.4	3.87
27	452	39.5	3.30
32	1,027	26.8	1.92
37	1,025	23.0	1.36

ment between measured and predicted insect population growth. For the published model, none of the intercepts was significantly different from 0 and only at 22.5°C and 12% grain moisture content was the slope significantly different from 1. The published model is thus shown to provide fairly good predictions over a broad range of environmental conditions.

A new model based on more extensive life history data might provide better predictions. Less life history data were available for *R. dominica* than for the 4 other major pests of wheat for which population growth models were developed (Hagstrum and Throne 1989, Hagstrum and Flinn 1990). A new egg production equation was based upon data collected at 42 combinations of grain moisture and temperature conditions, whereas the earlier equation was based upon only 10. With these additional data points, the new equation predicted higher egg production at both high and low temperatures. A new developmental time equation was based on data collected with only a whole-kernel wheat diet, whereas the earlier equation was based on data collected with 1 of several different grains or wheat flour as diets. Also, handling was reduced by determining only the total developmental time instead of the duration of each stage. Howe (1975) indicates that handling insects to determine the duration of instars generally increases developmental time. Using only whole-kernel wheat as a diet and determining only total developmental time probably explains the shorter developmental times observed in the current study.

With new egg production and developmental time equations, the new model predicted higher fecundities and shorter developmental times. The predictions of the new model were an average of 0.3–3.7 insects per kilogram of wheat closer to measured densities than those of the published model for different combinations of grain moisture and temperature. The biggest improvements tended to be under the extreme grain moisture and temperature conditions. Using the new model should not substantially change the overall conclusions of the earlier simulation studies on insect pest management done with the published model (Flinn and Hagstrum 1990, Hagstrum and Flinn 1990).

With the new model, none of the intercepts of measured against predicted regression equations

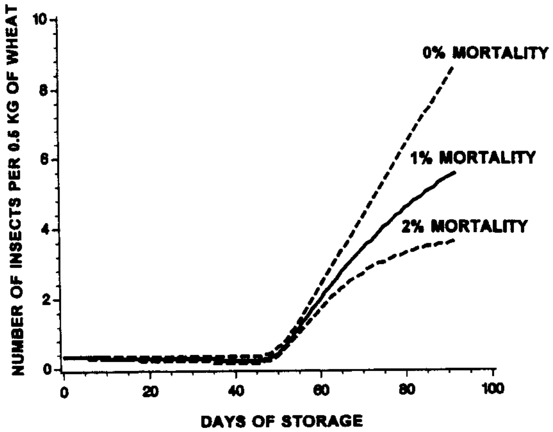

Fig. 4. Predicted *R. dominica* population growth at 27°C and 10.4% moisture with new egg production and new developmental time equations, and 0, 1, and 2% daily adult mortality rate substituted into published model (Hagstrum and Throne 1989).

was significantly different from 0, 6 of 8 of the slopes were closer to 1 than with the published model, and all of the standard errors of the slopes were smaller. The smaller standard errors are a result of closer agreement between measured and predicted insect densities. Slopes significantly different from 1 at the 1 or 5% levels in 3 cases were a result of these smaller standard errors. At 22.5°C and 12% moisture, the published model did not predict population growth better than the new model as suggested by the higher r^2 (0.96 versus 0.89), because the slope of 2.14 for measured against predicted regression indicated that the published model badly underestimates insect population growth.

The current study measured the growth of *R. dominica* populations over a broad range of grain moisture and temperature conditions. A published model predicted insect population growth over this range of environmental conditions fairly well. New egg production and developmental time equations predicted higher fecundities and shorter developmental times. Substituting these new equations

Table 3. First emergence of offspring and growth rate of *R. dominica* populations at 9 combinations of grain moisture and temperature conditions as predicted by new model

Temp, °C	% moisture	1st emergence, d	Growth rate, eclosion/d
22.0	10.0	103	0.032
22.5	12.0	82	0.074
23.0	13.1	75	0.111
27.0	10.4	47	0.116
27.5	11.5	41	0.178
27.5	13.5	38	0.326
31.0	10.4	33	0.183
31.0	11.5	31	0.292
31.5	13.5	27	0.386

and estimates of daily adult mortality rate in the published model improved predictions, particularly at extreme grain moisture and temperature conditions. The improvements of the model reported here increase its reliability as a pest management tool, and the additional validation of the model over a broader range of environmental conditions increases our confidence in its predictions.

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