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Predictability of Stored-Wheat Insect Population Trends from Life History Traits

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Environ. Entomol. 18(4): 660–664 (1989)

ABSTRACT The extent to which the relationship between environmental factors (temperature and grain moisture content) and life history traits can predict insect population trends in stored wheat was investigated by comparing nine measured population trends with predictions from population dynamics simulation models. Regression of measured against predicted insect population densities indicated that the predictions of the simulation model explained 87, 93, and 96% of the changes in the mean measured densities of *Cryptolestes ferrugineus* (Stephens), *Rhyzopertha dominica* F., and *Tribolium castaneum* (Herbst), respectively. Thus, for the population trends of the three species presented here, only 13, 7, and 4% of the changes in mean measured population densities remains to be explained by other factors.

KEY WORDS Insecta, stored wheat insects, life histories, simulation model

THE RELATIONSHIPS between environmental factors and life history traits are important to population ecologists because environmental factors influence population trends through their effects upon developmental time and egg production. Temperature and grain moisture content are major influences on the developmental time and egg production of stored-grain insects. Hagstrum & Milliken (1988) fitted equations to data from 45 published studies on the effects of these environmental factors on the developmental time of stored-grain insects. Data also are available on the effects of these factors on egg production by *Cryptolestes ferrugineus* (Stephens) (Smith 1965), *Rhyzopertha dominica* F. (Birch 1953), and *Tribolium castaneum* (Herbst) (Howe 1962). Earlier studies by Longstaff & Cuff (1984) used similar data to simulate the population trends of another stored-product insect pest, *Sitophilus oryzae* (L.). Population dynamics simulation models were used in this study to determine the extent to which the relationships between environmental factors (temperature and grain moisture content) and life history traits can predict population trends of three of the most important insect pests in stored wheat.

Materials and Methods

Population trends of single-species populations of *T. castaneum* and *R. dominica* were observed in the laboratory, and population trends of multiple-species populations of *C. ferrugineus*, *T. castaneum*, and *R. dominica* were observed in two cylindrical metal bins on a farm near Enterprise, Kans. Population trends from these two sets of data and a third set of data reported by Hagstrum (1987) were compared with population trends predicted by the population dynamics simulation models described in this paper.

Population Estimates. The study of insect populations in the laboratory was conducted in 19-liter (5 gal) metal cans (38 cm high, 30 cm diameter) containing 19 kg of hard red winter wheat. Three cans of wheat were infested with five pairs of adult *R. dominica* and two cans were infested with five pairs of adult *T. castaneum*. The study was conducted in a room maintained at 27°C and 70% RH (14% wheat moisture content). Nine samples of 0.12 kg of wheat were taken from each of the *T. castaneum* populations after 30, 50, and 70 d and from each of the *R. dominica* populations after 42, 56, and 70 d using a grain trier. The grain trier is a double-walled tube (2.5 cm outside diameter, 50 cm long) with seven oblong holes (1.5 by 5.4 cm). The inner tube is divided into seven compartments that collect grain samples when the inner tube is turned so that the holes in the two tubes match. In taking a sample, the holes are closed as the trier is pushed into the grain, they are opened to allow grain to enter the seven compartments, and then they are closed again before withdrawing the trier. One sample was taken in the center, four samples were taken near the edge of the container in four compass directions, and the other four samples were taken halfway between the center and edge sample locations. Adult insects were separated from the wheat with an oblong-hole grain sieve (0.18 mm by 1.27 cm) (Seedburo, Chicago) and counted.

On the farm, two cylindrical metal bins (6.4 m diameter), each with 82 t of hard red winter wheat 3 m deep, were sampled 3, 7, and 14 d after newly harvested wheat was placed in storage in late June and then at 2-wk intervals until the end of Sep-

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tember 1986 when the grain was fumigated. On each occasion, 24 2.9-kg samples of wheat were taken with a commercial pneumatic grain sampler (Cargill Probe-A-Vac, Minneapolis) from three locations near the center and three locations two-thirds of the distance between the center and outer wall in each of four vertical 0.75-m layers of grain. Adult insects were separated from the wheat with an oblong-hole grain sieve (Seedburo, 0.18 mm by 1.27 cm), identified to species, and counted. The average initial moisture levels of wheat samples was 10.4% in both bins, and moisture decreased 0.1% per week in the top and bottom layers but not in the middle layers. The average initial temperatures measured at sampling locations with thermocouple junctions spaced on cables at depth intervals of 0.9 m were 33.0 and 36.3°C, and temperatures decreased 0.7 and 0.8°C, respectively, per week.

Simulation Model. The population dynamics computer simulation model used in this study consisted of four major parts: equations describing the relationship between temperature and insect development, a delay process for moving the immature insects through the stages and simulating variation in developmental rate, a 70-element array for keeping track of adult age, and equations describing relationship between temperature and insect egg production. Insect survivorship was not explicitly included in the model. However, for *R. dominica* egg production was calculated in such a way as to include survivorship.

Temperature–developmental time equations used to calculate the time that insects spent in each stage were from Hagstrum and Milliken (1988). For *T. castaneum* and *C. ferrugineus*, significantly different temperature–developmental time equations had been fitted to data collected at high (14%) and low (10%) grain moisture contents. For these two species, the effects of intermediate moistures on developmental time were simulated by linear interpolation between the two calculated developmental times.

Variation in development rate was simulated with a time-varying distributed delay (Manetsch 1976). The basis for this method is that there is a mean (DEL) and variance (s^2) associated with the time required to complete development of a stage at a given temperature. The shape of the curve describing the number of individuals leaving a stage over time can be approximated by a member of the Erlang family of density functions. The specific function is designated in the model by the parameter K, which is calculated as DEL^2/s^2. There were few measures of variation in rate of development reported in the literature, so a variance was estimated for each mean duration of development using the equation of Shaffer (1983), where

$$s = 0.209\bar{x}^{0.73}.$$

A K for each stage was determined by first calculating a K for each temperature for which mean developmental times were available, then taking average of K's at the different temperatures. However, K for each stage was not allowed to exceed DEL*5, otherwise the delay would be unstable (i.e., would give erroneous results).

Eclosing adults, upon leaving the pupal stage, entered a 70-element adult array at a 1:1 sex ratio. Adults were moved each day to the next element of the array and were no longer considered in calculating egg production after 70 d.

Daily egg production rate was calculated using the equations in Table 1 based upon data for *C. ferrugineus*, *R. dominica*, and *T. castaneum* published by Smith (1965), Birch (1953), and Howe (1962), respectively. Daily egg production equalled the sum of the number of females multiplied by their daily lifetime average or age-specific egg production rate. For *R. dominica*, the equations described the effects of only grain temperature and moisture content on the daily average lifetime egg production rate, because insufficient data were available on age-specific changes in egg production. Daily egg production of *R. dominica* was calculated by dividing the rate of multiplication per generation (R_0) by the generation time (T) in days. For *T. castaneum*, egg production at 10% moisture was 60% of egg production at 14% moisture (Howe 1962) and for *C. ferrugineus* egg production at 10% moisture was 40% of egg production at 14% moisture (Smith 1965). Egg production rates at intermediate moistures were obtained by linear interpolation. Because White (1987) reported that daily egg production of *T. castaneum* on whole-kernel wheat was only half of that on the wheat flour and yeast diet used by Howe (1962), the egg production calculated using fitted equations was divided by two in the model.

Model inputs were the initial number of adult insects and the temperature and grain moisture conditions for each day of the simulation. Because estimates of initial population densities were quite variable for farm bins, all simulations were begun with five pairs of adults. The predicted numbers for each sampling date were then adjusted, so that for each of the populations the sums of predicted equalled the sums of mean measured population densities. This procedure used all of the measured mean densities for each population to establish what the initial population density must have been.

We used programs from the SAS Institute (1982) to fit regression equations for egg production and to calculate means and standard errors for each of nine insect populations on each sampling date. Bonferroni *t* tests (Milliken & Johnson 1984) were performed to compare measured with predicted mean population densities. An SAS regression program also was used to compare measured and predicted mean population densities.

Results and Discussion

The measured population trends of three species of adult stored-grain insects were quite similar in

Table 1. Equations describing egg production (Y) in relation to age of adults (A), and temperature in °C (T) for two species of stored-product insects and temperature and percentage of grain moisture (M) for *R. dominica*

Species	df	Equation[a]	r^2
C. ferrugineus[b]	72	$Y = e^{0.76T-0.026T^2-0.00062T^2A+0.38A-0.034A^2-4.38}$	0.8729
R. dominica	9	$Y = 1.45T - 0.024T^2 + 0.37M - 24.64$	0.8086
T. castaneum[b]	40	$Y = e^{-23.96 \text{ LOG } T+8.70T-0.43T^2-0.00022T^2A+0.0085T^3+5.41}$	0.9359

[a] Equations for *C. ferrugineus*, *R. dominica*, and *T. castaneum* are based upon data published by Smith (1965), Birch (1953), and Howe (1962), respectively.
[b] $T = T - 19$°C.

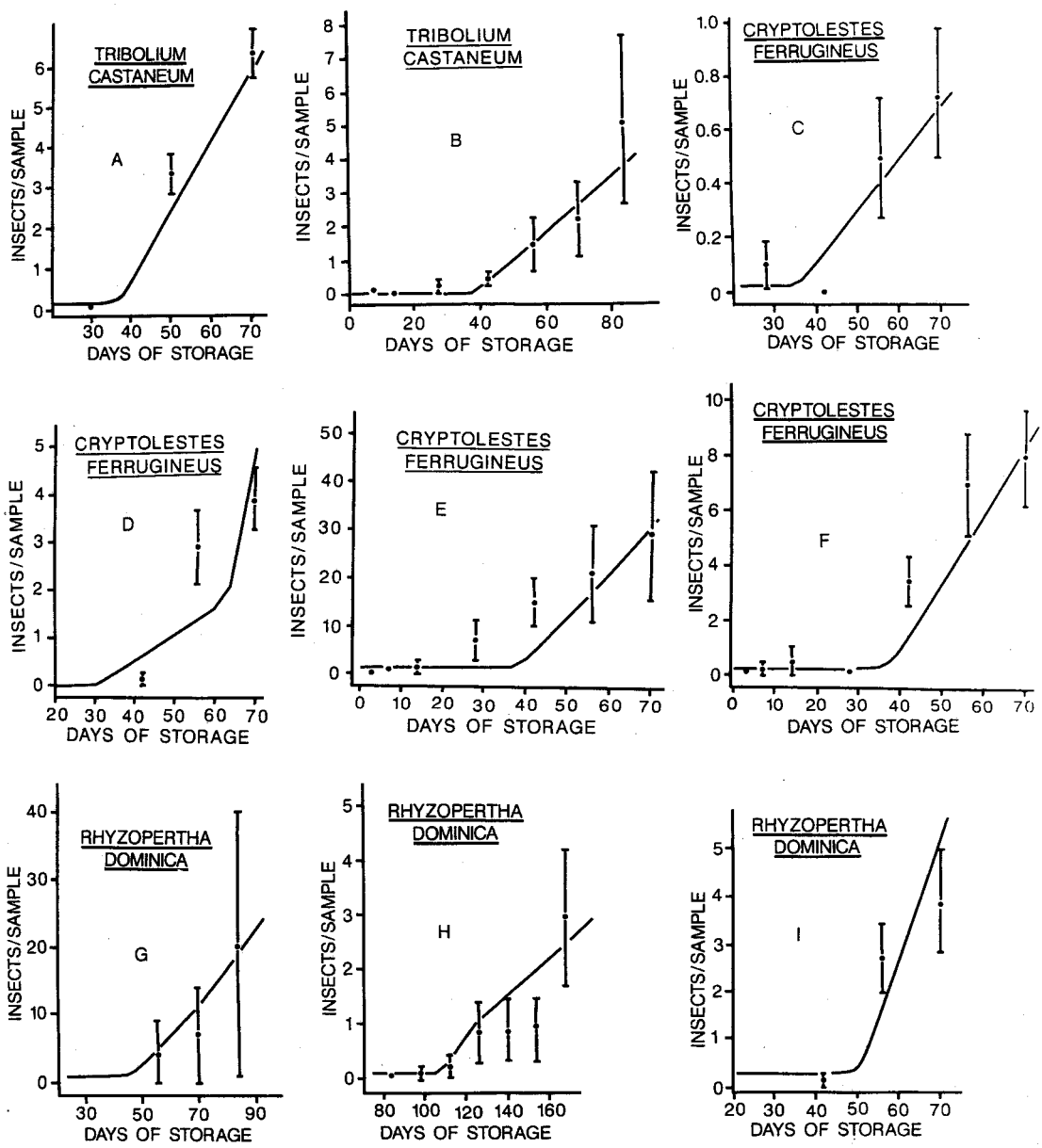

Fig. 1. Comparison of measured seasonal changes in the mean number of adult insects per sample (·) ± SE (vertical bar) with the numbers of insects predicted by the simulation model (——). The population trends include new laboratory data (A and I), new on-farm data (B, E–G), and on-farm data (C, D, and H) collected by Hagstrum (1987).

Table 2. Parameters for regression of measured (y) against predicted (x) population densities for three insect species

Parameter	Species		
	C. ferrugineus	*R. dominica*	*T. castaneum*
df	20	12	9
Slope ± SE	1.01 ± 0.088	0.95 ± 0.078	1.12 ± 0.081
t for H0: slope = 1	0.1474	−0.576	1.502
Probability > t	0.8843	0.5753	0.1673
Intercept ± SE	0.95 ± 0.72	−0.30 ± 0.51	0.052 ± 0.20
t for H0: intercept = 0	1.320	−0.579	0.254
Probability > t	0.2025	0.5743	0.8056
R^2	0.8750	0.9309	0.9603

form (Fig. 1). Few insects were found in samples during the first 30 to 33 d for *C. ferrugineus;* 35 and 38 d for *T. castaneum;* and 42, 48, and 102 d for *R. dominica*. The only adults present during this initial period were those that were introduced during initial infestation in laboratory studies (Fig. 1A and I) or those that immigrated into newly harvested wheat stored on the farm (Fig. 1B–H). The duration of this period of low initial density was generally determined by the developmental times for a species. However, a much longer 102-d period of low adult numbers for *R. dominica* (Fig. 1H) was probably the result of either delayed immigration of this species into the bin or the first-generation adults being too scarce to be found in samples taken. After a period of low initial adult insect densities, the adult population then increased rapidly as the offspring of these initial adults reached the adult stage.

The measured mean insect population densities increased as the predicted population densities increased (Fig. 1). When the Bonferroni t test was used to compare measured mean population densities to predicted, the differences were not significant at the 1% level for any of the nine populations. However, in some cases, the large standard errors of measured mean densities may have been responsible for the lack of significant differences. Another approach to comparing means, regression of measured (y) against predicted (x) insect population densities, indicated that the simulation model explained 87, 93, and 96% of the changes in mean measured densities of *C. ferrugineus*, *R. dominica*, and *T. castaneum*, respectively (Table 2). Thus, for population trends of the three species presented here, only 13, 7, and 14% of the differences between predicted and measured mean population densities remains to be explained by other factors. A slope of <1 indicated that the predicted densities tended to exceed the measured densities of *R. dominica*, whereas a slope of >1 indicated that the measured densities of *C. ferrugineus* and *T. castaneum* tended to exceed predicted densities. However, none of the slopes were significantly different from 1. Also, the intercepts of regression equations were not significantly different from zero for any of the three species, indicating that as densities approached zero, neither measured nor predicted densities were consistently higher or lower than one another. Consistently high survivorship is not too surprising under the favorable conditions encountered in this study. The similarity between measured and predicted numbers of insects per sample is particularly encouraging in that these comparisons include data from four different bins of farm-stored wheat, from two different crop years, and from single- and multiple-species populations.

This capability to predict insect infestation levels from the initial adult density and the expected grain temperature and moisture conditions can be valuable in evaluating the relative effectiveness of various pest management programs. Thorpe et al. (1982) used a simulation model to study the effects of aeration on *S. oryzae*. However, with stored grain, pest management decisions often must be made for several insect species simultaneously. The next step is to validate the model over a wider range of environmental conditions and to add various management practices such as parasites, aeration, fumigation, and insecticide applications. With such further development, the models described here should be useful in evaluating the relative effectiveness of a pest management program on different pest species.

Acknowledgment

We thank Jeff Daniels, an electrical engineering student at Kansas State University, for help with computer programming.

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Received for publication 17 June 1988; accepted 5 December 1988.