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A Predictive Mathematical Framework for Simulating Rusty Grain Beetle Infestation in Bulk Wheat Storage

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The rusty grain beetle, *Cryptolestes ferrugineus* (Stephens) (Coleoptera: Laemophloeidae), is a serious pest of stored wheat because its numbers can rise quickly when the thermal environment is favorable. The purpose of this study was to develop a compact mathematical framework for describing and forecasting changes in beetle abundance in bulk wheat. Population history was considered together with temperature and accumulated thermal exposure, expressed as effective degree-days. Observations from different storage-patch sizes and from constant as well as changing temperature regimes were examined. Nine unstructured population equations were first tested. Key-factor analysis was then used to identify the variables most closely associated with population change, after which these variables were combined with the degree-day response. None of the nine simple population formulations gave a satisfactory fit across all of the experimental conditions. A three-parameter sigmoidal function described the relationship between accumulated heat units and insect abundance most consistently. The final model used the population recorded at the previous observation, the effective degree-day total over 28 days, and temperature fluctuation. It reproduced the main pattern of population increase under both constant and changing temperatures, with the most useful predictions occurring before the infestation approached its maximum density. The results suggest that a model which retains both thermal history and population history can provide a practical forecasting tool for *C. ferrugineus* in stored wheat.

Keywords Cryptolestes ferrugineus · Rusty grain beetle · Population dynamics · Mathematical modeling · Stored wheat · Degree-day model · Fluctuating temperature · Pest forecasting · Stored-grain protection

1 Introduction

Population growth in stored grain is not controlled by a single environmental variable. Temperature, food availability, duration of storage, grain volume, and the number of insects already present can act together to determine how quickly an infestation develops. The rusty grain beetle, *Cryptolestes ferrugineus*, is especially important in stored wheat because favorable temperatures can allow its population to increase rapidly [1,6,7,10]. A reliable description of this increase is useful when decisions about monitoring and control have to be made before the infestation becomes severe.

The size of the grain mass also matters. Earlier studies of *C. ferrugineus* reported differences in population development among storage volumes and showed that the population present at an earlier stage can affect abundance at a later stage [1,2]. In a bulk store, temperature is also spatially variable and may change more slowly inside the grain than in the surrounding air [6,7]. Consequently, insects in different parts of a grain mass may experience different thermal histories even during the same storage period.

A number of mathematical models have been used to represent population change, ranging from exponential and logistic descriptions to discrete-time density-dependent and harvesting models. Such equations are useful because they reduce a biological process to a small number of interpretable parameters. Their performance, however, can deteriorate when temperature, population density, and storage conditions change together [2,3,8]. For stored-grain prediction, the challenge is therefore to retain the variables that matter most without making the model unnecessarily complicated.

Detailed demographic models can separately describe development, reproduction, mortality, and different life stages. They can provide valuable biological insight, but the amount of information required to parameterize

them may limit their direct use in large storage facilities. A simpler equation based on variables that can be measured during routine monitoring may be more useful when the practical objective is to estimate whether an infestation is approaching a damaging level [2,8,21].

Key-factor analysis offers a useful intermediate approach. Rather than attempting to represent every demographic mechanism, it identifies the factors that explain a substantial part of the observed variation in population size. These factors can then be incorporated into a comparatively small predictive equation [4]. This approach is particularly attractive when experimental data contain several environmental treatments but the final model is intended for practical use.

Thermal conditions are central to insect development because insects depend strongly on environmental temperature. Degree-day methods provide a convenient way of summarizing temperature exposure as accumulated heat units and have long been used in insect development and phenology studies [14–18,22]. The difficulty arises when temperature changes substantially through time, because a relationship obtained under constant temperature may not transfer directly to a fluctuating environment.

The thermal behavior of bulk wheat adds another source of variation. A grain mass can buffer short-term changes in ambient temperature, so the temperature experienced by insects inside the bulk may differ from the temperature recorded outside the storage unit. Population development may therefore reflect the combined influence of accumulated heat, temperature variation, population density, and storage scale rather than degree-days alone [5,6,19].

This study was designed to develop a practical prediction framework for *C. ferrugineus* in bulk-stored wheat. Nine unstructured population models were compared first. Key-factor analysis was subsequently used to determine the main contributors to population change, and the resulting variables were combined with a degree-day relationship. The final framework was examined under constant and changing temperature conditions, with particular attention to its ability to predict population growth before the infestation reached its maximum level.

2 Mathematical formulation of population growth models

To investigate the population response, alternative mathematical descriptions were formulated using insect abundance together with storage-patch size and thermal conditions. The equations represent different assumptions about reproduction, density dependence, mortality, and environmental influence. Their ability to reproduce the observed adult counts at successive observation periods was then compared.

For model calibration, the observed number of adults was converted to an estimated female population by using a 1:1 sex-ratio assumption. Accordingly, one-half of the observed adult count was treated as the main population variable. This follows the population-modeling procedure adopted in earlier work on *C. ferrugineus* [2].

Nine unstructured formulations were examined. The set covered continuous and discrete growth as well as density-dependent, density-independent, harvesting, and lagged formulations. The aim was not to select a universal population law, but to determine whether any of these relatively simple equations could capture the observed infestation pattern across the storage treatments.

Model performance was judged from the coefficient of determination (R^2) and the residual mean square error (RMSE). A larger R^2 together with a smaller RMSE indicated better agreement with the observations. Where two equations gave similar statistical performance, the simpler equation was preferred because fewer parameters are easier to estimate and interpret.

Case I: Geometric growth with a carrying capacity

$$\frac{dN}{dt} = aN\left(1 - \frac{N}{K}\right) ----(1)$$

Case II: Exponential growth under continuous reproduction

$$N_t = N_0 e^{at} ----(2)$$

Case III: Geometric growth with discrete generations

$$N_t = N_0 \mu^t ----(3)$$

Case IV: Density-dependent population growth with instantaneous feedback

of density on total growth

$$N_t = K + \left[\frac{k-N_0}{N_0}\right] e^{-at} \text{--------(4)}$$

Case V: Density-dependent population growth with delayed feedback

$$N_{t+1} = N_t e^{r(1-\frac{Nt}{k})} - - - -(5)$$

Case VI: Harvest-based population model for pest suppression

$$\frac{dN}{dt} = aN\left(1 - \frac{N}{k}\right) - EN \quad - - - -(6)$$

Case VII: Discrete-time density-dependent population model

$$N_{t+1}/N_t = \frac{R_0}{1 + [\frac{R_0 - 1}{k}]N_t} - - - -(7)$$

Case VIII: Density-independent discrete-time population model

$$N_{t+1} = R^{\alpha} N_t - - - - - - - (8)$$

Case IX: Density-independent model with a two-period lag

$$N_{t+2} = R^{\alpha} N_t - - - - - - - (9)$$

In the equations, N_t represents one-half of the number of living adults at time t, while N_0 is one-half of the initial living-adult count. The symbols t + 1 and t + 2 refer to the next observation period and the following period, respectively; in this study, each period represents 28 days. The parameter a denotes the intrinsic growth rate, μ is the geometric growth factor, K is the carrying capacity, and R_0 represents the net reproductive rate.

t + 2 is next two periods (28 days per period in this study), *a* is the intrinsic growth rate, μ represents the geometric growth factor where *k* is the carrying capacity, and R_0 is the net reproductive rate

For every formulation, measured and calculated half-adult populations were compared using R^2 and RMSE. Applying the same two measures to all nine models allowed their predictive performance to be compared on a common basis.

3 Key-factor analysis

Key-factor analysis was applied to determine which measured variables were most closely related to changes in *C. ferrugineus* abundance, following the general approach of Morris [4]. Regression relationships were fitted to the observed population data, and alternative combinations of temperature, previous population size, and temperature variation were examined.

$$\text{Log}_{10}N_{t+1} = A\text{Log}_{10}N_t \text{---------(10)}$$

$$\text{Log}_{10}N_{t+1} = A\text{Log}_{10}N_t + \text{Log}_{10}F \text{---------(11)}$$

$$\mathrm{Log}_{10}N_{t+1} = A\mathrm{Log}_{10}aN_t + \mathrm{Log}_{10}F \text{---------(12)}$$

$$\mathrm{Log}_{10}N_{t+1} = A\mathrm{Log}_{10}aN_t + \mathrm{Log}_{10}F + B \text{---------(13)}$$

In these equations, B is the regression coefficient, $\log_{10}F$ represents the contribution of the factor term, a describes survival under the corresponding temperature treatment, and C represents the remaining or comparatively minor contribution of other factors.

The temperature treatment was therefore retained as an important component of the analysis, while C was treated as the smaller residual contribution not explained by the principal factors.

The fitted relationships were evaluated using R^2 and RMSE. When two candidate equations showed similar values, the formulation requiring fewer fitted parameters was retained. Both complete and incomplete data sets were examined to determine whether a meaningful crowding effect was evident.

4 Degree-day model

Thermal exposure was evaluated by relating population abundance to the accumulated effective degree-days. The analysis considered total adults, living adults, and offspring separately when the corresponding observations were available. This made it possible to examine whether a common temperature-based relationship could describe the different measures of population abundance.

The sum of degree days was found as $DD = \sum_{t=0}^{N}$ (T_t-6.3) --------(14)

Here, T_t is the grain temperature on day t, expressed in °C, and 6.3 °C is the threshold temperature used in the calculation. This threshold corresponds to the minimum movement temperature reported for adults of *C. ferrugineus* [25] and was therefore used as the lower limit for calculating effective thermal accumulation.

The 6.3 °C threshold was used to represent the onset of measurable activity in the beetles. Daily temperatures above this value contributed to the accumulated heat-unit total, which was subsequently related to population abundance through regression analysis. The resulting relationship was then compared across the different temperature treatments.

5 Key factor–degree-day model

The key-factor and degree-day analyses were brought together to describe population change over approximately one generation. The population in the next observation period was assumed to depend mainly on the population already present and the amount of effective heat accumulated during the preceding 28 days.

Separate regression relationships were estimated for live adults, total adults, and offspring under the constant-temperature treatments. Key variables were added in stages so that their contribution to the prediction could be assessed. The resulting expressions were then adjusted for application to the temperature-increase and temperature-decrease treatments.

The equation giving the strongest overall statistical performance, judged primarily by higher R^2 and lower RMSE, was selected for subsequent prediction under the temperature-increase and temperature-decrease conditions.

6 Results and discussion

6.1 Unstructured population models

Across the storage conditions examined, none of the nine unstructured population equations consistently reproduced the observed half-adult abundance. Their limited performance indicates that a single population-growth mechanism was insufficient to represent the combined effects of thermal conditions, population history, and storage scale.

At constant temperatures of 25 °C and above, temperature alone did not appear to be the main constraint on population increase [1]. The results instead point to an important role for the population already present and for the size of the storage patch. This agrees with the view that population history and spatial scale can influence infestation development in stored grain [1,2].

In the large storage patch, none of the tested equations adequately described the insect counts at 25 and 30 °C. At 35 °C, however, Cases I, IV, and V gave comparatively good fits. This change in model performance with

temperature indicates that the dominant population process was not constant across the experimental conditions.

Model	Grain Container	Temperature of Grain(C)					
		21	25	30	35	T-increase	T-decrease
Case I	Small patch	0	0.30	0.10	0.02	0	0.80
	Medium patch	0	0.44	0	0	0.77	0.35
	Large patch	0	0	0.33	0.93	0.55	0.34
Case II	Small patch	0	0	0	0	0	0
	Medium patch	0	0	0	0	0	0
	Large patch	0	0.59	0	0	0	0
Case III	Small patch	0	0	0	0	0	0
	Medium patch	0	0	0	0	0	0
	Large patch	0	0.59	0	0	0	0
Case IV	Small patch	0	0	0	0.28	0	0
	Medium patch	0	0	0	0.37	0.93	0rt
	Large patch	0	0	0	0.74	0.95	0.25
Case V	Small patch	0	0.52	0	0.94	0	0.69
	Medium patch	0.67	0.95	0	0.96	0	0.96
	Large patch	0.71	0	0	0.88	0	0.98
Case VI	Small patch	0.24	0.16	0.08	0.03	0.28	0.47
	Medium patch	0.53	0.12	0.01	0.04	0.48	0.26
	Large patch	0.56	0.52	0.01	0.30	0.25	0.30
Case VII	Small patch	0	0	0	0	0	0.27
	Medium patch	0	0	0	0	0	0
	Large patch	0	0	0	0	0	0
Case VIII	Small patch	0	0	0	0	0	0
	Medium patch	0	0.55	0.11	0.20	0.70	0
	Large patch	0	0.50	0.50	0	0.48	0
Case IX	Small patch	0	0	0	0	0	0
	Medium patch	0	0.10	0	0.13	0.39	0
	Large patch	0	0	0	0	0	0

Table 1. R^2 values obtained for the nine unstructured population models fitted to one-half of the total number of living C. ferrugineus adults.

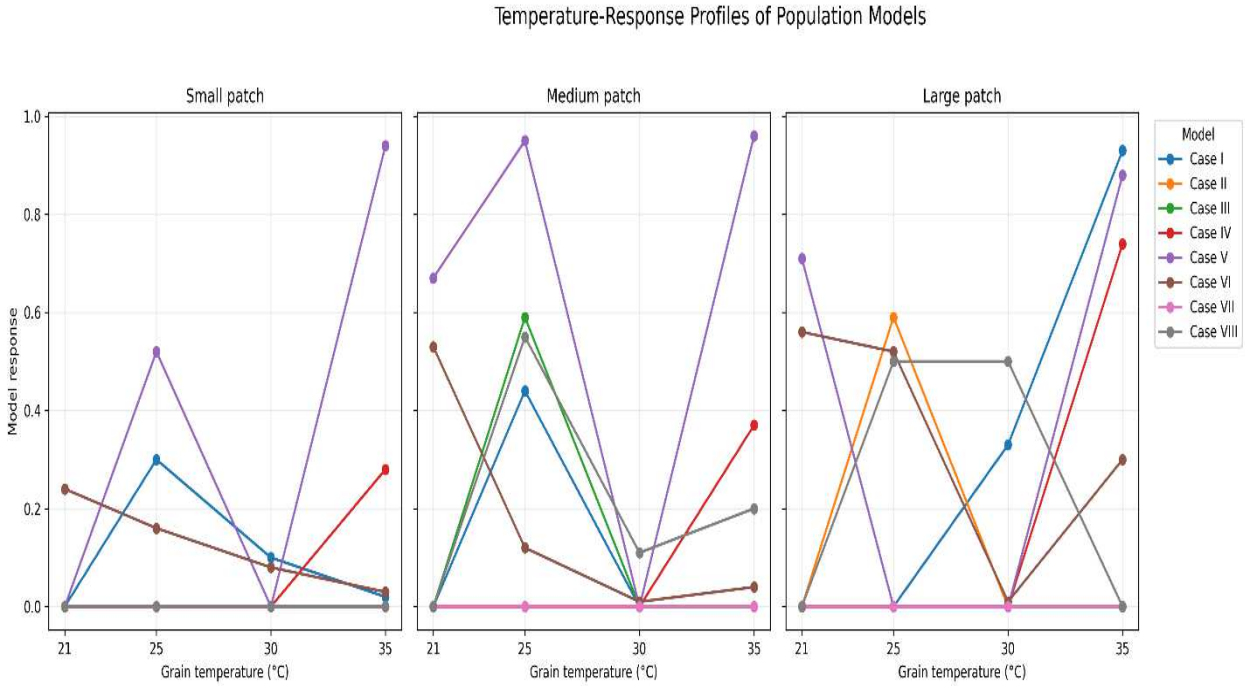


Fig. 1. Performance of the unstructured population models across the tested storage conditions.

6.2 Key-factor analysis

For the temperature treatments examined, Eq. (11) gave the most consistent regression relationship. The results also indicated that populations at temperatures of 30 °C or below had not yet reached their maximum density. This suggests that, during the observed growth phase, the previous population and thermal conditions could still provide useful information for predicting subsequent abundance.

Data	Temperature (°C)	Regression parameters			
		F_a (approx)	B_b (approx)	R^2 (approx)	RSME
Complete data of Live adults	25 30 35	84.84 393.30 1,727.55	0.44 0.26 0.19	0.62 0.36 0.37	674.26 1,800.70 4492.70
Complete data of all insect number	25 30 35	49.76 386.61 3,202.92	0.55 0.37 0.23	0.67 0.95 0.60	1,073.88 1,187.67 10,000.36
Incomplete data of Live adults	25 30 35	54.31 107.32 34.36	0.51 0.51 0.78	0.78 0.97 0.99	507.73 501.23 845.13
Incomplete data of all insect number	25 30 35	14.52 552.96 3,202.92	0.72 0.33 0.23	0.94 0.88 0.60	465.66 1,771.56 10,000.36

Table 2. Regression results for Eq. (11) using observations from the large storage patches.

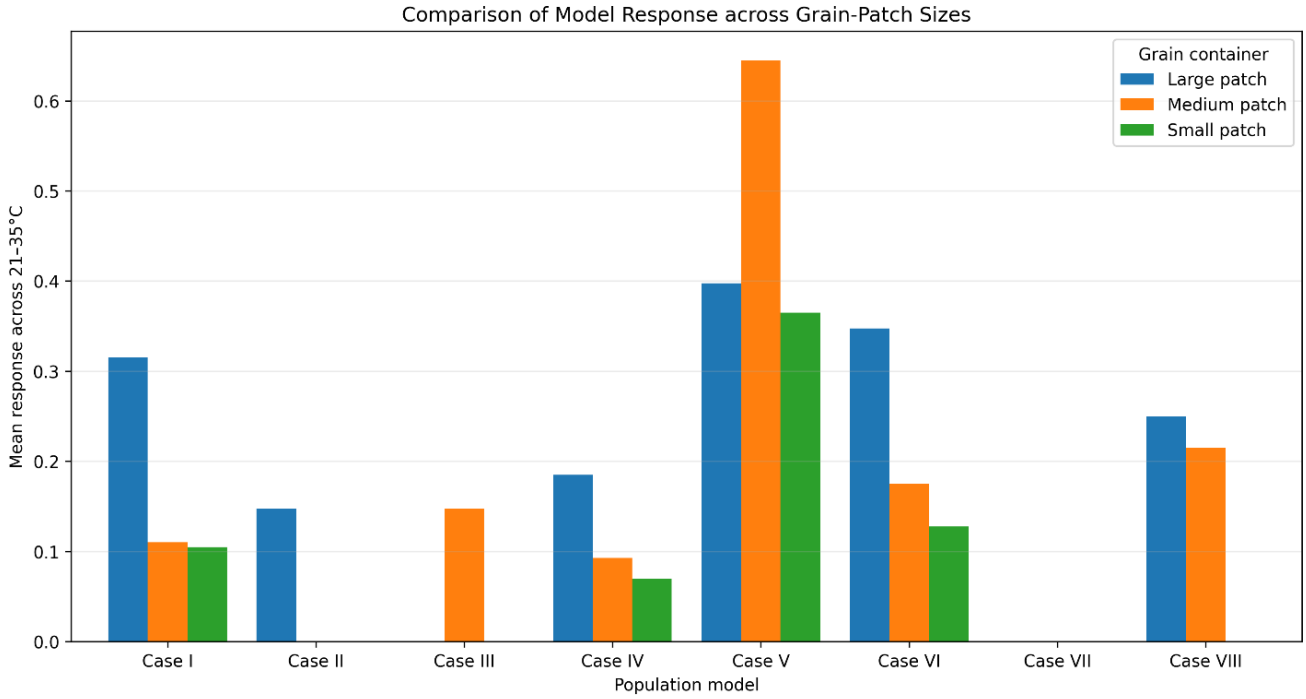


Fig. 2. Regression relationship obtained from the key-factor analysis for the large-patch data.

6.3 Degree-day model

During the period before maximum density was reached, adult abundance generally increased as effective degree-days accumulated. The pattern was most evident in the large storage patches and in treatments where temperature was changed during storage.

Across the constant, increasing, and decreasing temperature regimes, the three-parameter sigmoidal function provided the most satisfactory description of the relationship between accumulated degree-days and insect abundance. The result indicates that population increase was not indefinitely proportional to thermal accumulation; rather, the response gradually changed as the population approached higher densities.

$$\text{Sum numbers of adults} = C/1+\exp\,[-(\text{Sum Degree Day}-P_o)/D] \quad \text{----------(16)}$$

Here, C, D, and P_o are fitted constants, with their values allowed to vary among temperature treatments. The equation was used to estimate total adult abundance from the accumulated degree-day total. The same form was then examined for its ability to represent the population response over the different thermal conditions.

days and the total number of adults under all the tested constant temperatures and inside the large patches , the best-fitted equation was-

$$\text{Sum numbers of adults } = C/1 + \exp[-(\text{Sum Degree Day} - Po)/D(T - 6.3)c] \ldots (17)$$

$$R^2 = 0.87\,,\ RMSE = 2{,}345.3 \text{ where } C = 3{,}538.592 + 2{,}624.015,$$
$$D = 5.268 + 14.619, c = 1.614 + 0.816,\ P0 = 4{,}902.226 + 1{,}124.974$$

The degree-day relationship captured the broad pattern of population increase under both constant and fluctuating temperature regimes. Its limitations became more apparent when a relationship fitted only to constant-temperature observations was transferred to changing temperatures, where abundance tended to be overestimated. This result supports the inclusion of temperature variation and population history in the final predictive model.

6.4 Key factor–degree-day model

The final model was formulated to predict live adults, total adults, and offspring in the large storage patches. It combines the population observed at the preceding time point with the effective degree-days accumulated over 28 days and a term representing temperature fluctuation. The purpose of this formulation was to retain the variables that showed the strongest predictive contribution while avoiding unnecessary model complexity.

$$\mathrm{Log_{10}N_{t+1}} = \mathrm{A + BX + C + \frac{DX}{1+EXLog_{10}\,N_t}} \quad \text{------ (18) where T increase or constant}$$

$$\mathrm{Log_{10}N_{t+2}} = \mathrm{A + BX + C + \frac{DX}{1+EXLog_{10}\,N_t}} \quad \text{, Where T decrease or constant}$$

In Eq. (18), the insect numbers after 28 and 56 days and at the beginning of the observation period are represented by the corresponding population terms. X denotes the effective degree-day sum over 28 days, while A, B, C, D, and E are fitted parameters. Parameter values were estimated separately for the relevant temperature conditions and population measures.

Parameters	Insect numbers used for equation 18		
	Live adults(approx)	All adults(approx)	Offspring(approx)
A	−2.1281	−1.3450	−1.6287
B	0.0066	0.0049	0.0071
C	1.4112	0.7525	1.0725
D	−0.0015	−0.0008	−0.0014
E	0.0002	−0.0009	0.0008
R^2	0.91	0.96	0.83
RMSE	9.2	14.7	4.6

Table 3. Estimated parameters of Eq. (18) for C. ferrugineus populations.

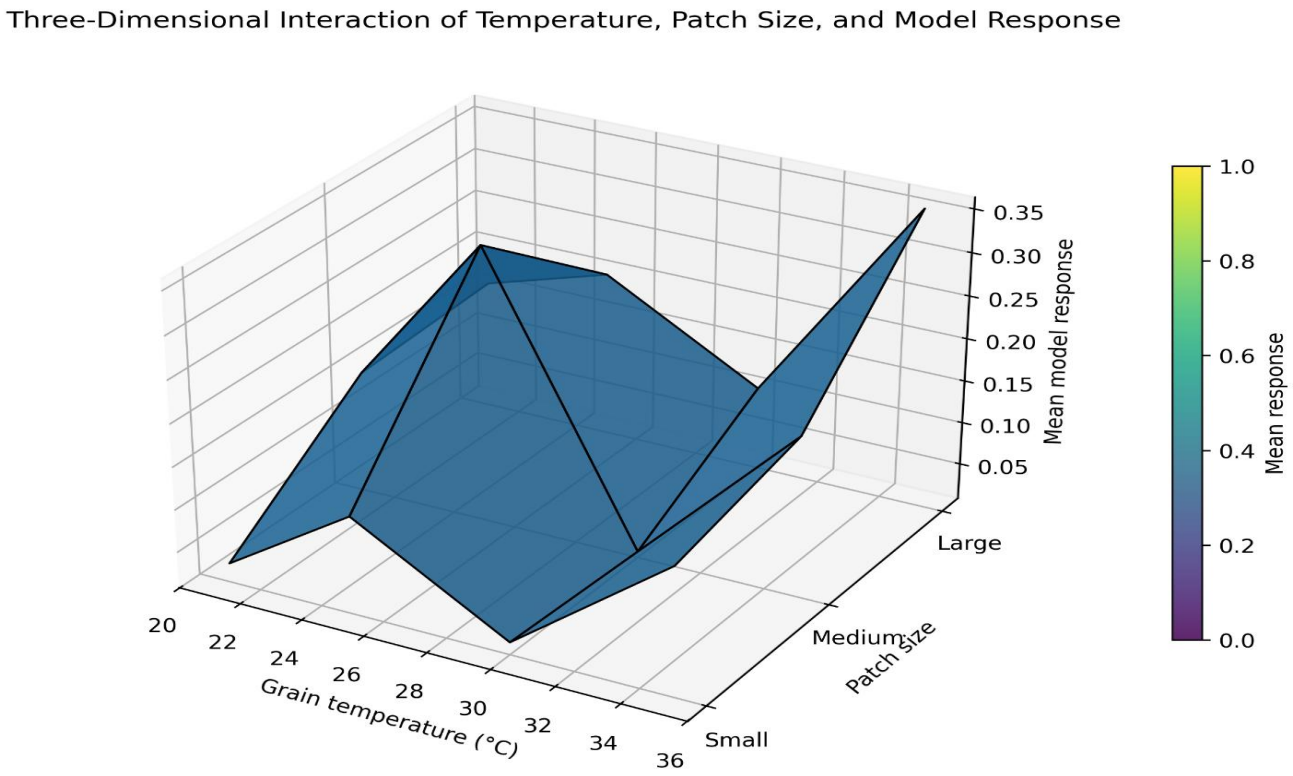


Fig. 3. Observed and predicted insect abundance from the key factor–degree-day model.

The final equation reproduced the broad behavior of live adults, total adults, and offspring under both constant and fluctuating temperatures. The parameter estimates in Table 3 gave R^2 values of 0.91 for live adults, 0.96 for total adults, and 0.83 for offspring, with corresponding RMSE values of 9.2, 14.7, and 4.6, respectively. These results indicate that the combined model retained a substantial amount of the observed variation and was particularly useful during the period preceding peak population density.

7 Conclusions

The comparison of the nine unstructured population equations showed that none could adequately describe *C. ferrugineus* abundance across all of the tested storage conditions. Of the alternatives considered, the three-parameter sigmoidal relationship gave the most consistent description of the association between accumulated thermal exposure and insect abundance. The analysis further showed that temperature, temperature fluctuation, and the population present during the preceding observation period were important contributors to subsequent population development.

Including these variables in the key factor–degree-day framework improved the model's ability to follow population growth, particularly before the infestation reached its maximum density. The proposed formulation therefore provides a relatively simple way to translate routinely measured thermal and population information into an estimate of future beetle abundance. Further validation with independent storage data would be needed before the model is used as a general forecasting tool across other wheat-storage systems.

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Declarations

Conflict of interest: The authors declare that they have no conflict of interest.

Data availability: The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

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