Neural Computing and Applications
https://doi.org/10.1007/s00521-023-09020-y

ORIGINAL ARTICLE

Modeling reproductive fitness of predator, *Hippodamia variegata* (Coleoptera: Coccinellidae) using support vector machine (SVM) on three nitrogen treatments

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Received: 25 December 2021 / Accepted: 5 September 2023

Abstract

Protein and carbohydrate content in the diet of the predator *Hippodamia variegata* Goeze (variegated ladybug) directly influences reproduction fitness by affecting foraging efficiency. The effect of three varied qualities of *Aphis gossypii* Glover (cotton aphid) prey on daily *H. variegata* feeding and daily egg production (DEP) were estimated using the support vector machine (SVM). The SVM can predict predator reproductive behavior as a function of the relationship between foraging and prey nutritional composition. We used the total number and weight of aphids consumed, volume of protein, lipid, carbohydrate, and glycogen, and total energy received by the ladybug after feeding on one prey item as input variables. Aphid quality varied as nitrogen (N) fertilization levels were 110, 160, and 210 ppm on the *Cucumis sativus* L. (cucumber) host plants. The model estimated female beetles consumed more aphids and nutrients on *C. sativus* plants with N levels of 160 ppm compared to lower (110 ppm) N levels and had higher reproductive transformation efficiencies. Transformation rates of aphid feeding to egg production in females exposed to the 160 ppm treatment were 65% greater, had lower nutrient and energy requirements, and achieved a 29.4% higher DEP than those exposed to high (210 ppm) N levels. The SVM predicted nutrient compositions of *A. gossypii* exposed to 160 ppm N were balanced such that *H. variegata* exhibited greater reproduction efficiency than the other N treatments for first 30 d from the start of reproduction.

Keywords Genetic algorithm · Predation efficiency · Predator reproduction efficiency · Prey nutritional content · Support vector machine (SVM)

Abbreviations

ANN	Artificial neural network
Avg	Average
Carb	Carbohydrate
Const	Constant
DEP	Daily egg production, $\hat{y}$
GA	Genetic algorithm
Gly	Glycogen
Lip	Lipid
MAPE	Mean absolute percent error
N	Nitrogen
P	Protein
Poly	Polynomial
Q_p	Number aphids consumed/eggs produced
R^2	Coefficient of determination
R	Reproduction
RBF	Radial basis function
RMSE	Root mean squared error
TC	Total daily aphid consumption
TE	Total energy
SVM	Support vector machine
V	Variance
TCw	Consumed aphid weight

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Published online: 29 September 2023

1 Introduction

Foraging tactics that affect reproductive fitness in animals is mediated by food suitability [1–6]. The proportion of certain macronutrients (i.e., protein, lipid, and carbohydrate) consumed by animals is often associated with fitness attributes such as longevity, reproduction, and growth [7–12]. Macronutrient balance is the primary dietary determinant for foraging and reproductive performance (fitness) based on a host of data accumulated over the past two decades from laboratory studies of several model species including *Drosophila melanogaster* (fruit fly) [7–11], *Acheta domesticus* (house cricket) [12, 13] and *Parasteatoda tepidariorum* (house spider) [14–17]. Kouloussis et al. [11] linked protein and carbohydrate intake to daily egg production (DEP) in *Ceratitis capitata* Wiedemann (Mediterranean fruit fly) to identify proportions of each for the optimization of fly reproductive fitness.

Nitrogen fertilization, a common agricultural practice, alters nutritional qualities of plants and subsequently affects third level (predator) dynamics [18–24]. Knowledge of the nutritional requirements needed by a given predator is critical to mass rearing and release for high-efficiency biological control programs. The importance of prey nutritional quality on Coccinellids, the most utilized predators in agroecosystems and greenhouses for biological control of aphid species because of their foraging efficiency [e.g., 20, 23, 25, 26] and reproductive success [e.g., 5, 24, 27] has been frequently studied. However, no empirical model has been generated to illustrate the role macronutrient composition of natural prey species plays in reproductive fitness of *Hippodamia variegata*.

Several research groups have used a multivariate response-surface factor to estimate the linear or nonlinear effect of various protein to carbohydrate consumption ratios from artificial diets on daily macronutrient production in a chosen insect using time units [7, 9, 13]. With this approach, the test subject (model insect) shows a preference for particular nutrients and resultant fitness outcomes correlating with its preference can be measured [31]. To examine individual macronutrient contributions from natural prey to predator performance, the predator is not given a selection of varied nutrients but rather its dependency level to nutrients is explored. Exploring a host of treatments based on natural prey is not practical due to the labor intensity required by each experiment and limited treatment results capable of being produced. Ensuant data could be expanded upon with predictions from machine learning. SVM has been widely used to identify an independent output effect from each input variable in a complex system such as the predator–prey relationship utilizing one prey item. Fuzzy logic, a feature of soft computing, is a useful tool for managing uncertainties inherent to complex (natural prey) systems [28] as it exploits imprecision tolerance, uncertainty, and partial or degrees of truth to achieve tractability, improve robustness, lower solution costs, and provides a better rapport with reality [29, 30]. Kernel machines, and associated learning methods such as the support vector machine (SVM) approach [31], represent one of the most important directions both in theory and application of soft computing. SVM is able to make full use of a plethora of systems data. Originally developed by Vapnik [31], SVM, is applied to complex data types beyond feature vectors (e.g., graphs, sequences, and relational data) by designing kernel functions. This algorithm minimizes generalization error and minimizes overfitting to achieve a generalized performance [32].

A gap exists in the literature regarding the effect prey nutritional value has on predator daily reproduction. This lack of information reinforces the need for comprehensive studies to highlight the contributions of each macronutrient (input variables) from *Aphis gossypii* in DEP (output variable) in *H. variegata* using SVM.

The variegated ladybug has been identified as an important natural enemy preying upon aphid species including *A. gossypii*, which negatively impact many different agricultural crops [1, 33–36]. The quality of *A. gossypi* on *Cucumis sativus* varied with nitrogen fertilizer application rates and was useful for predicting *H. variegata* reproductive behavior. The contribution of each macronutrient input variable for SVM was measured as the nutritional proportion of one prey item consumed by the predator. The combined input variables for SVM were total aphid consumption (TC), weight of aphid consumption (TCw), protein (P), lipid (L), carbohydrate (Carb) along with glycogen (Gly), and total energy received by a predator through feeding one prey item (TE). Following SVM estimations, a genetic algorithm (GA) would be used to estimate the daily number of *A. gossypii* necessary for maximum reproductive fitness of *H. variegata* across three different nitrogen treatments. The GA is a heuristic technique based on the principals of natural selection and genetics [37] which can efficiently find approximate solutions more quickly than classic methods. Studies of population evolution can continue through successive generations with GA providing satisfactory predictions regarding resulting conditions [38, 39]. The specific goals of the present research were to: (1) Determine the linear or nonlinear relationship between *A. gossypi* nutritional inputs and *H. variegata* reproductive rate in terms of its daily foraging (consumption); (2) Predict the treatment, including optimal macronutrients proportions, leading to the maximum daily reproductive rate of *H. variegata*; (3) Optimize *H. variegata* reproductive rates under conditions

of differing daily prey availability; and (4) Establish the model parameters required to achieve the purposes of this study.

In this study we aim to investigate whether prediction and optimization of reproductive behavior in the commercialized variegated ladybug (*H. variegata*) can be of use in controlling the globally distributed aphid, *A. gossypii*. Our hypothesis is that evaluation of ladybug performance metrics (prey consumption, rate of reproduction, etc.) will provide vital information regarding nutrient loads that must be met for optimal reproductive performance and prey consumption when *H. variegata* is used as a biocontrol.

2 Materials and methods

2.1 Prey (*A. gossypii*) and predator (*H. variegata*) culture, input and output variable assays

The experimental system consisted of *C. sativus* (cucumber) as the feeding source for prey, *A. gossypii* (cotton aphid), with the variegated ladybug *H. variegata* as predator. Nitrogen fertilization rates within the system were kept at three levels; 110, 160, and 210 ppm, representing leaf protein concentration levels [assessed in Hosseini et al. 23]. Cotton aphids were collected from colonies naturally infesting cucumber plants in the research greenhouse at Ferdowsi University of Mashhad, Mashhad, Iran. Adult ladybugs were collected from aphid-infested cucumbers cultivated in a research greenhouse. The stock colony of beetles was maintained in a climate-controlled growth chamber set to 25 ± 1 °C, 70 ± 10% RH, and a 16:8 (L:D) photoperiod. To predict reproductive behavior of *H. variegata* in relation to daily consumption for three N treatments using SVM, data from our previous studies including DEP for *H. variegata* females fed with *A. gossypii* [5] and macronutrient analysis of *A. gossypii* at three N treatments was used [23]. Three separate stock colonies of adult ladybugs were established with each being fed aphids exclusively from one specific N treatment for a single generation. A total of 60 ladybug eggs were studied for each N treatment from egg eclosion. The number of eggs produced, adult survival, and the number of aphids killed by beetles each day, were recorded until the death of each beetle. In our previous study [23], total aphid macronutrient content (protein, carbohydrate, lipid, and glycogen) increased with N fertilization rates.

2.2 Support vector machine (SVM)

Support vector machines (SVM), similar to artificial neural networks (ANN), are a method of data-mining used to isolate, identify, and classify a particular data set [40–42]. Here, SVM was used to model DEP of the predator, *H. variegata*. Seven independent variables, though one was combined with another, were collected from each female ladybug beetle: lipid (L), protein (P), total energy (TE), carbohydrate (Carb) and glycogen (Gly), total aphid consumption (TC), and weight of aphid consumption (TCw) (Fig. 1). Also, using the designed SVM model, DEP of the predator for each nitrogen treatment was plotted and the effects of independent variables were studied. Use of SVM us advantageous because of the high computational speed, good generalization, quadratic programming approach to problem-solving, and its transparency feature; all reasons why we chose this approach. To accomplish our research objectives, the least square support vector machine (LS-SVM) was used. This SVM adaptation uses the least-squares error-function with a goal of estimating $\hat{y}$ (daily egg production, DEP) in terms of x (independent variables):

$$\hat{y} = \sum_{k=1}^{m} \overline{\alpha}_k . K(\mathbf{x}, \mathbf{x}_k) + b \tag{1}$$

where $\overline{\alpha}_k = \left(\alpha_k - \alpha_k^*\right)$, $\mathrm{K}(\mathrm{x}, \mathrm{x}_k)$ is the inner product of input vector (x) and support vector (x_k) where b is the bias term.

To calculate $\alpha^* = \left(\alpha_1^*, \alpha_2^*, \ldots, \alpha_k^*\right)^T$ and $\alpha = (\alpha_1, \alpha_2, \ldots, \alpha_k)^T$, optimization Eq. (2) needs to be solved.

$$\begin{cases} \sum_{i,k} (\alpha_i - \alpha_i^*)(\alpha_k - \alpha_k^*) K(x_i, x_k) + \varepsilon \sum_{i=1}^{k} (\alpha_i + \alpha_i^*) - d \sum_{i=1}^{k} (\alpha_i - \alpha_i^*) \\ \text{subject to} \\ \sum_{i=1}^{k} (\alpha_i - \alpha_i^*) = 0 \text{ and } \alpha_i, \alpha_i^* \in [0, C] \end{cases} \tag{2}$$

where ε and C are the hyper-parameters.

Two kernel function types, polynomial and radial basis function (RBF) were used.

$$K(x_i, x) = \exp\left(\frac{\|x - x_i\|^2}{\sigma^2}\right) \tag{3}$$

$$K(x_i, x) = [(x * x_i) + 1]^d \tag{4}$$

where $\sigma > 0$ is kernel width and d is the polynomial degree ($d = 1, 2, 3$).

2.3 Genetic algorithm (GA)

Genetic algorithms (GAs) are a class of heuristic optimization algorithms that are inspired by the process of natural selection. They can be used as global search

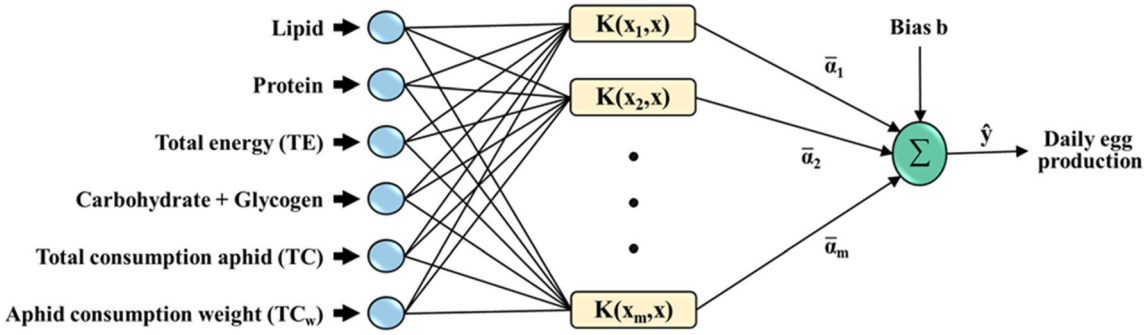

Fig. 1 SVM model components used for estimation of daily egg production (DEP)

techniques to solve complex optimization problems by simulating the evolution of a population of candidate solutions [37]. GA carries out a fitness-based selection and recombination process inspired by natural selection to generate a new population of solutions from the previous one [43]; this iterative process continues until satisfactory conditions are met [38], as illustrated in Fig. 2.

In this study, we focus to identify the optimal nutritional requirements for ladybug beetles that would result in maximum daily (24-h) egg production throughout their lifespan. To achieve this goal, we used a GA optimization algorithm to explore different combinations of aphid consumption rates of the ladybugs. The first step was to measure the number of aphids consumed by the beetles during a 24-h period of maximum egg production under three different N treatments. This provided us with a baseline for the aphid consumption rates, which was used as a starting point for the GA optimization. Next, the egg production rates of the beetles under two different scenarios were measured: A constant and variable value of total number of aphids consumed (TC) throughout the lifetime of *H. variegata*. By comparing the egg production rates under these two scenarios, we were able to determine the effect of different consumption scenarios on the beetle's reproductive success. In the first scenario of our GA optimization, we assumed that the optimized aphid consumption was a constant daily number. This allowed us to explore different combinations of aphid consumption rates under the assumption of a fixed daily consumption rate. In the second scenario, we treated the optimized aphid

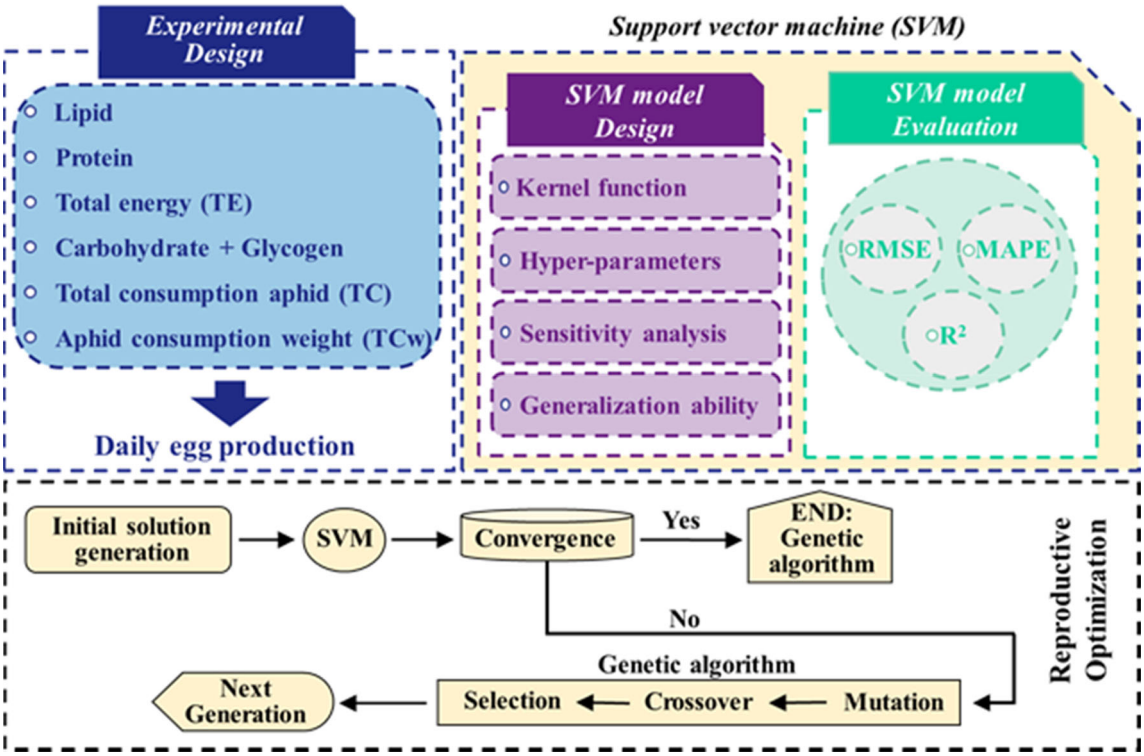

Fig. 2 Schematic overview of daily egg production (DEP) modeling and optimization using GA algorithm

consumption as a variable daily number, allowing us to explore solutions that varied the daily consumption rate. During the GA optimization process, we made the assumption that prey nutrient and energy proportions were constant. This enables us to focus on optimizing the aphid consumption rates without the added complexity of considering changes in prey nutrient composition. The SVM model was utilized as a fitness function in the GA. The GA algorithm started by randomly generating a set of solutions for the independent variables. These solutions were evaluated using the SVM model, which produced a fitness score for each solution. In each subsequent generation, the GA algorithm created a new set of possible solutions by applying selection, crossover, and mutation operators to the fittest solutions from the previous generation. The selection operator chose the best-performing solutions from the previous generation to serve as parents for the next generation. The crossover operator combined the genetic material of the selected parents to create new offspring solutions. The mutation operator introduced random changes to the offspring solutions to explore new regions of the search space. The fitness of the new solutions was evaluated using the SVM model, and the fittest solutions were selected to serve as parents for the next generation. This iterative process continued until the GA algorithm reached a stopping criterion, such as a maximum number of generations or a convergence in the fitness scores of the solutions. The optimization process is illustrated in Fig. 2. This genetic algorithm uses tournament selection, intermediate crossover, and adapt feasible mutation, with an elite number of 5, 1500 generations, a population size of 50, a crossover probability of 0.5, and a migration probability of 0.1.

2.4 Reproductive fitness of *H. variegata*

Our objective was to extract SVM design parameters to interpret the daily egg production (DEP) of the ladybugs under three different treatments. By utilizing the SVM model, we were able to analyze the egg production data and identify the factors that influenced the onset of oviposition and the duration of peak production. To provide a visual representation of the results, we created three-dimensional surface plots to illustrate the onset of oviposition and the duration of peak production for each of the three treatments. These surface plots allowed us to identify any differences in the timing and duration of egg production between the treatments and explore the factors that influenced these patterns. Additionally, we employed the GA optimization algorithm to identify the maximum egg production rates for ladybug beetles under daily varied or constant-number prey availability for three 15-day time periods of adult female longevity. By testing different combinations of aphid consumption rates and feeding conditions, we were able to identify the optimal feeding strategy for maximizing daily egg production rates over the lifespan of the ladybug beetles. We presented the results using optimization graphs, which showed the relationship between aphid consumption rates and egg production rates for each of the three time periods. The optimization graphs enabled us to identify the feeding conditions that maximized egg production rates for each of the three time periods. We found that the optimal feeding strategy varied depending on the time period, with different combinations of aphid consumption rates and feeding conditions producing the highest daily egg production rates at different stages of the ladybug beetles' lifespan.

2.5 Statistical analysis of variable and constant reproduction data of *H. variegata*

Variable and constant reproduction data for *H. variegata* consuming prey from the three N fertilization treatment groups were compared using one-way ANOVA followed by the Tukey–Kramer test to separate means when F-values were significant. Data were tested for normality and homogeneity of variance using Kolmogorov–Smirnov and Bartlett tests, respectively [44].

3 Results

3.1 Model performance evaluation

To calculate our coefficient of determination (R^2) for SVM, the nutritional input variables TC, TCw, P, L, Carb and Gly, and TE for each N treatment were evaluated using four different kernel functions including radial basic function (RBF), linear, polynomial degree 2 (Poly2) and polynomial degree 3 (Poly3). The analysis showed that the RBF kernel was the best function for all nutritional training data set sizes. The statistical parameters used to evaluate SVM accuracy during the train, test, and total phases for each N treatment are presented in Table 1. SVM predicted percent variation in beetle DEP with a maximum train error of 4.74, 8.12 and 9.91 in N fertilization treatments of 110, 160, and 210 ppm. Root mean square error (RMSE) was less than 0.5 for all data. Examination of p values, mean comparisons, and variance and statistical distribution of the experimental and predicted data sets indicated SVM can effectively predict beetle DEP for all phases. No significant differences were observed in the experimental data. Therefore, using SVM the relationship between nutritional input and egg production in *H. variegata* is predictable.

The plots of predicted and experimental values from two train and test phases for three N treatments are depicted in

Table 1 Estimated daily egg production (DEP) in *H. variegata* for three N treatments using SVM

	Treatment	110 ppm N			160 ppm N			210 ppm N		
		Train	Test	Total	Train	Test	Total	Train	Test	Total
	RMSE	0.14	0.13	0.14	0.43	0.48	0.43	0.34	0.42	0.35
	MAPE	4.74	4.04	4.67	8.12	8.48	8.15	9.91	4.48	9.40
Average (Avg)	Experimental	2.70	2.89	2.72	7.69	8.61	7.78	6.66	7.54	6.73
	Predicted	2.69	2.87	2.71	7.76	8.73	7.86	6.63	7.43	6.70
	P value	0.96	0.97	0.95	0.93	0.97	0.92	0.97	0.97	0.96
Variance (V)	Experimental	1.36	0.7	1.29	22.75	34.37	23.47	15.73	27.62	16.41
	Predicted	1.31	0.82	1.25	20.14	32.93	21.01	14.15	26.82	14.91
	P value	0.88	0.83	0.91	0.62	0.97	0.64	0.72	0.98	0.73
Skewness	Experimental	1.01	0.99	0.99	0.90	0.27	0.82	0.46	0.27	0.46
	Predicted	1.07	0.46	1.03	0.89	0.30	0.83	0.48	0.35	0.48
	P value	0.99	0.93	0.99	0.40	0.88	0.25	0.99	0.99	0.99

Fig. 3. The results showed a very good fit, $R^2 > 0.98$, between predicted and experimental values for beetle DEP in all N treatments. Linear regression lines, slopes, and intercepts were approximately equal to 0 and 1, respectively.

3.2 Weighted input attributes for prediction of *H. variegata* daily egg production (DEP)

Lifetime DEP in *H. variegata* for three N treatments was estimated with SVM giving attribute weights to input variables. These weights could establish the importance of each variable for prediction of DEP. Figure 4 illustrates the R^2 values obtained from experimental and predicted data sets. Attributes with absolute weight values > 0.50, were considered very important predictors [32]. Therefore, in the 110 ppm N treatment, TCw and TE were the most effective predictors of female beetle DEP. Aphid P and Carb and Gly levels were the primary predictors of DEP in 160 ppm N treatments. All classified input variables were more than 80% accurate predictors of DEP in 210 ppm N treatments.

3.3 Evaluation of reproductive responses in *H. variegata*

Nonlinear relationships between mean DEP (output) and female beetle reproductive age in days (input) in relation to weight of aphids consumed (input), and the input variable with the highest R^2 value for each N treatment were determined. The resultant data were depicted in three-dimensional surface plots (Fig. 5). The highest reproductive responses to the 110 ppm N treatment were obtained when greater numbers of aphids were consumed shortly after the onset of oviposition. As these beetles aged, rates of reproduction slowed. Based on the curves, TE acquired from aphid prey was the limiting factor for reproduction in the 110 ppm N treatment group.

Female beetles treated with 160 ppm N had higher levels of reproduction over longer time periods than those in the 110 ppm N treatment group. According to the SVM prediction, two reproductive peaks corresponding with the middle (25) and high (35) numbers of aphid consumption were found in the 160 ppm N treatment group. Daily P intake, rather than TC, was the most integral input variable for predicting reproductive behavior in this group.

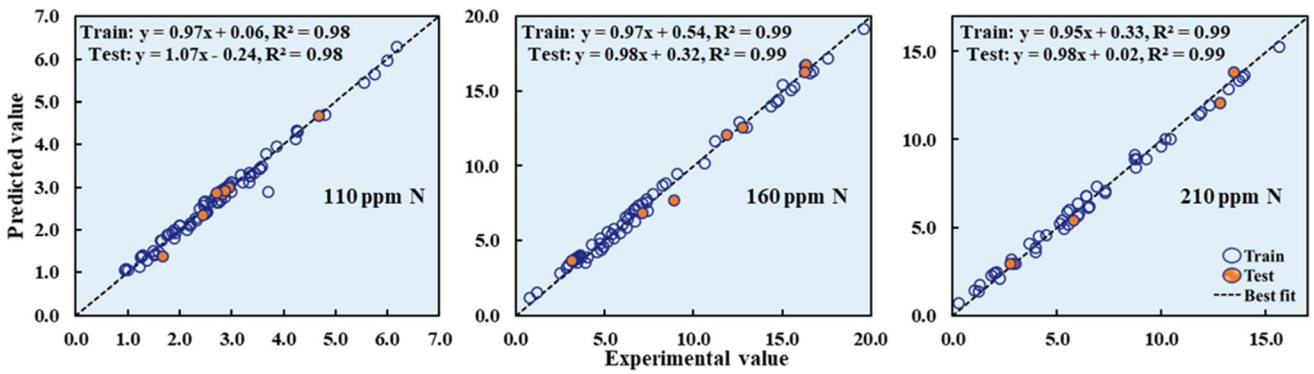

Fig. 3 Predicted versus actual daily egg production values in *H. variegata* for 110, 160 and 210 ppm N treatments

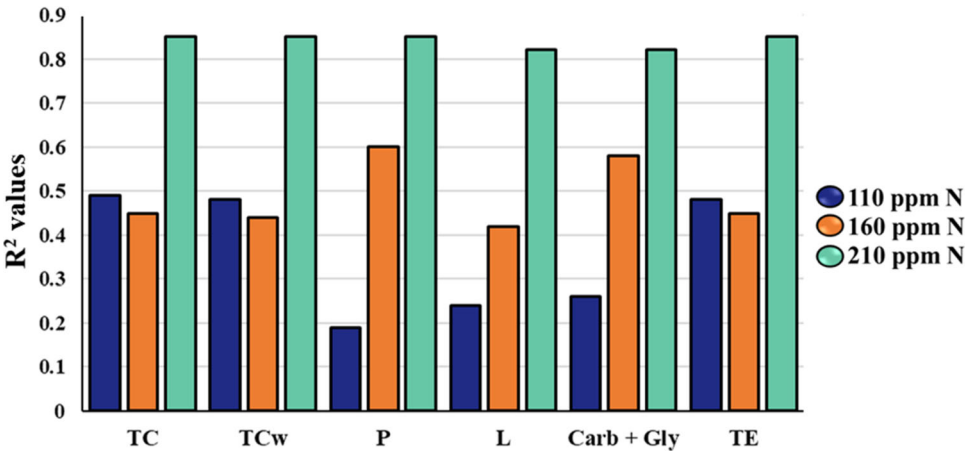

Fig. 4 Evaluation of attribute weights for nutritional variable inputs on prediction of daily egg production in *H. variegata* at three N treatments. Total number of aphids consumed (TC), total weight of aphids consumed (TCw), protein from aphid body (P), lipids from aphid body (L), carbohydrate and glycogen of aphid body (Carb + Gly), total energy from aphid body (TE)

The highest N treatment group, at 210 ppm, showed the duration of peak production was recorded when between 17 and 35 aphids were consumed daily. Despite the large volume of aphid intake, mean DEP dropped quickly as the beetles aged. There was no ideal variable at this treatment level as all input variables showed the high degree of confidence for prediction of reproductive behavior.

3.4 Optimizing reeding requirements in *H. variegata*: a genetic algorithm-SVM approach

The primary objective of optimization in this study was to maximize *H. variegata* reproduction by considering all independent variables. To achieve this, we employed a GA with a SVM model as the merit function. We selected six variable features, including the total number of aphids consumed (TC), total weight of aphids consumed (TCw), protein from aphid body (P), lipids from aphid body (L), carbohydrate and glycogen of aphid body (Carb + Gly), and total energy from aphid body (TE). Moreover, we included the variable of the day for optimization, resulting in a total of seven variables that were optimized to identify the feeding conditions that would yield the highest *H. variegata* reproduction, specifically, the maximum number of eggs produced per day. These optimized conditions were used to generate the results presented in Table 2, which provide valuable insights into the feeding requirements of *H. variegata*. Our analysis revealed that the greatest number of eggs were produced on day 21, 14, and 18 for the 110, 160, and 210 ppm N treatments, respectively. It is interesting to note that female beetles in the 210ppm treatment group consumed the highest number of aphids, macronutrients, and trace elements. However, our results demonstrated that the females in the 160 ppm N treatment group produced the highest number of eggs per day. This finding suggests that a moderate concentration of nutrients may be optimal for maximizing egg production in *H. variegata*. While a higher concentration of nutrients may increase aphid consumption rates and overall nutrient intake, it may not necessarily lead to higher egg production rates per day. Our results provide valuable insights into the feeding requirements of *H. variegata* and can inform the development of effective pest management strategies that promote the species' reproductive success.

In the previous optimization scenario, all growth variables of female *H. variegata* were optimized to maximize reproduction, but the resulting approach was not applicable due to the difficulty in defining a single diet for *H. variegata* throughout its life. To address this challenge, a new optimization scenario was hypothesized, where the dietary ration of *H. variegata* could vary to suit its growth needs as it grew larger. To implement this scenario, we kept the optimization variable of the day constant and carried out the optimization process individually for each day. Specifically, we performed the optimization process 240 times for all three nitrogen treatments during the 80-day period from the 5th to the 84th day. In summary, the first optimization scenario resulted in a constant value of total number of aphids consumed (TC) throughout the lifetime of *H. variegata*, while in the second scenario, TC was optimized for each day to achieve the maximum reproductive output on that particular day. The comparison of these two scenarios is presented in Fig. 6, which provides valuable insights into the impact of dietary optimization on the reproductive success of *H. variegata*. The results of our study demonstrate that the optimal values of total number of aphids consumed (TC) should vary throughout the lifetime of *H. variegata* to achieve maximum reproductive success. This indicates that the ideal feeding conditions may differ from day to day and cannot be achieved through a constant diet throughout the insect's life. Additionally, the total amount of nutrition required under the variable feeding mode is significantly lower than that required under constant feeding conditions. Notably, the optimal nutritional requirements for *H. variegata* differ for each of

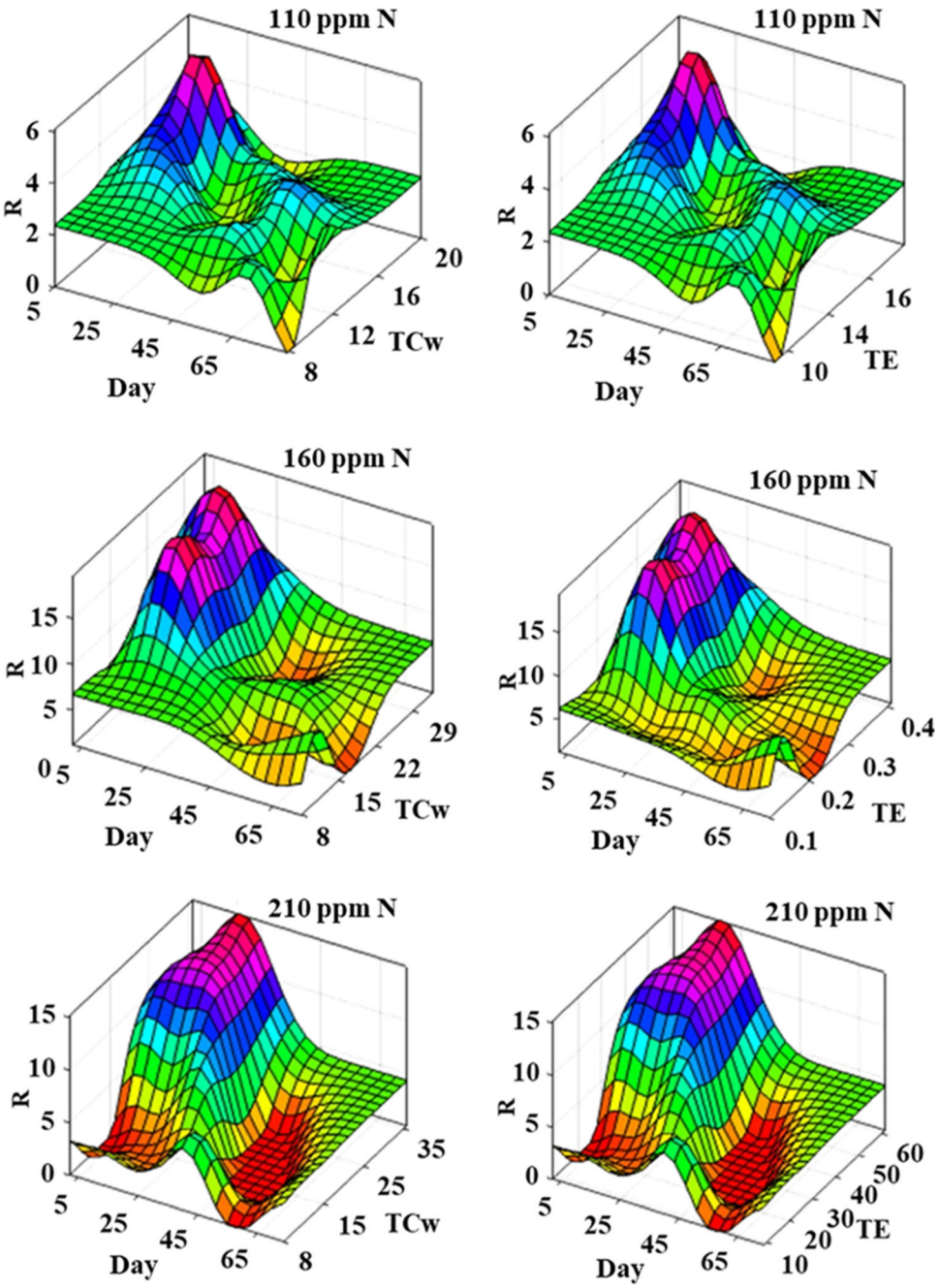

Fig. 5 Nonlinear relationship between mean total reproduction (R) of *H. variegata* and reproductive age (Day) in relation to weight of aphids consumed (TCw), and the input nutritional variable the highest R^2 estimated by SVM for N treatments at 110, 160 and 210 ppm

Table 2 Optimization of *H. variegata* reproduction using a GA-SVM approach at different nitrogen treatment levels

Nitrogen treatment	Day	TC	TCw	P	L	Carb + Gly	TE	R	Q_p
110	21	45.28	16.81	0.21	0.22	0.42	18.66	6.75	8.04
160	14	71.66	26.66	0.38	0.50	0.88	39	19.42	3.69
210	18	75.49	31.78	0.54	0.73	1.10	54.60	13.71	5.5

TC total number of aphids consumed, *TCw* total weight of aphids consumed, *P* protein from aphid body, *L* lipids from aphid body, *Carb + Gly* carbohydrate and glycogen of aphid body, *TE* total energy from aphid body, *R* reproduction, O_p transformation rate from aphids consumed to eggs produced

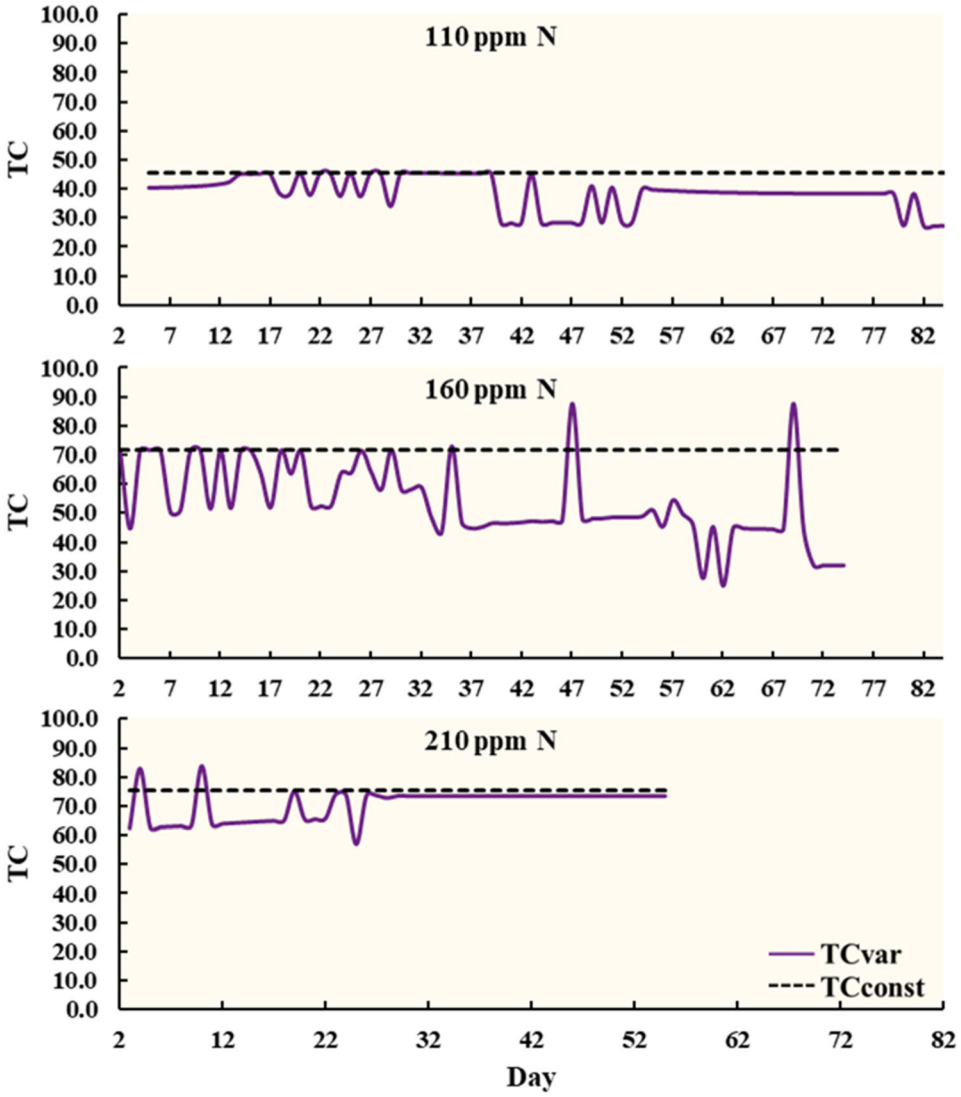

Fig. 6 Optimization of feeding conditions for maximizing daily egg production in H. variegata at different nitrogen treatment levels (110, 160, and 210 ppm) under constant (TCconst) and variable (TCvar) feeding scenarios

the three nitrogen treatments tested, highlighting the importance of tailoring feeding conditions to the specific growth requirements of the insect. These findings have significant implications for the development of efficient and sustainable feeding strategies for *H. variegata* in the field of insect rearing and biocontrol.

The present study investigates the impact of two feeding scenarios, constant (TCconst) and variable (TCvar), on the reproductive changes of *H. variegata* over time. The results are presented in Fig. 7, which shows that the trends of reproductive changes in both scenarios are similar, yet the amount of reproduction is significantly higher in the TCvar scenario. This can be attributed to the appropriate nutrition provided to H. variegata throughout its life under the variable feeding regime. Notably, the highest amount of reproduction occurred in all three nitrogen treatments between 15 and 20 days, after which the trend of reproductive changes starts to decline and remains almost constant. Interestingly, during this period of constant reproduction, the TCvar scenario resulted in a significantly higher amount of reproduction compared to TCconst. These findings suggest that *H. variegata* is capable of maintaining reproduction to an acceptable extent under variable feeding conditions, highlighting the importance of this feeding method for optimizing reproduction in this species.

We conducted a study to compare the daily egg production (DEP) and aphid consumption of H. variegata under two feeding scenarios for three nitrogen treatments. Using optimization results obtained from the GA, we found that the 110 ppm N treatment resulted in the consumption of 3087 and 3622 aphids in the TCvar and TCconst scenarios, respectively. The TCvar scenario led to a higher number of eggs produced (338) compared to the TCconst scenario (268). Similar results were observed for the 160 ppm N treatment, where the DEP was higher in the TCvar

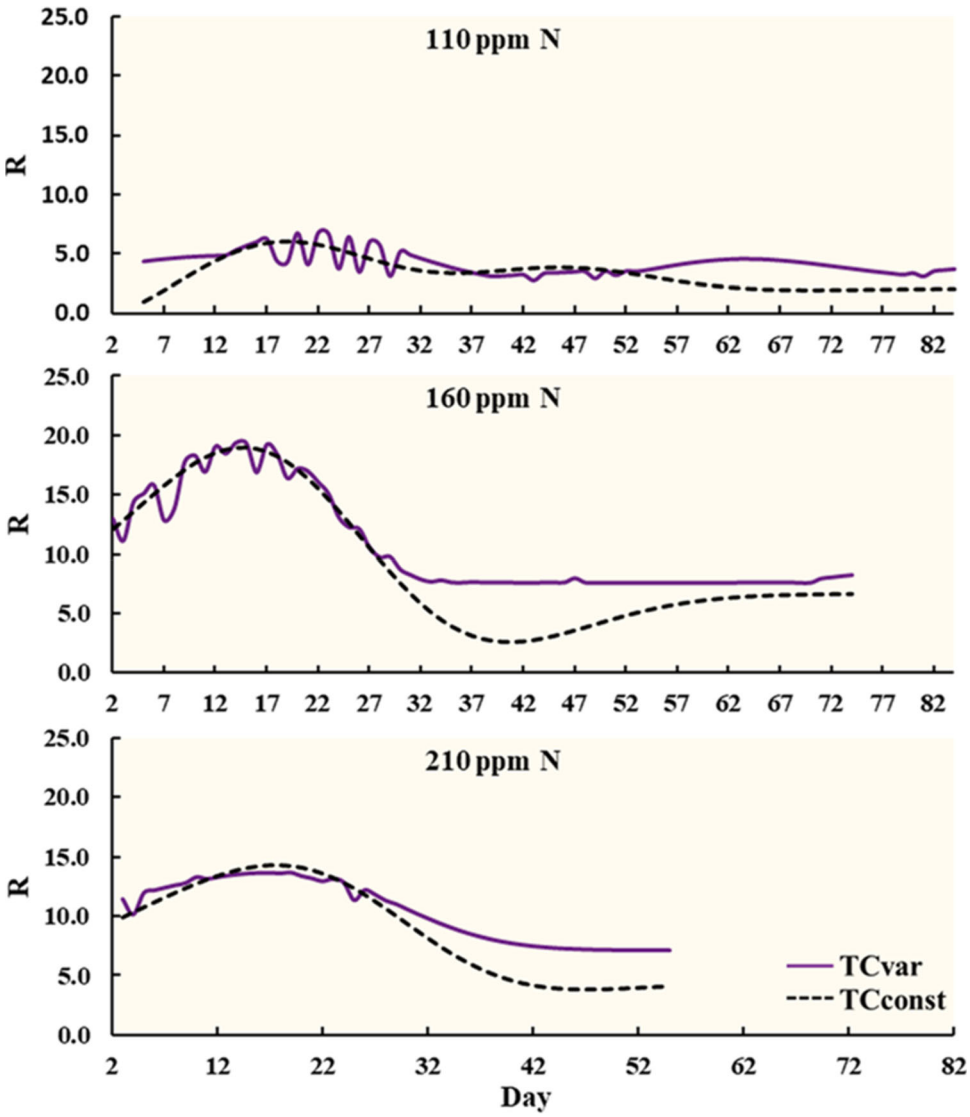

Fig. 7 Optimization of reproduction (R) in H. variegata at different nitrogen treatment levels (110, 160, and 210 ppm) under constant (TCconst) and variable (TCvar) feeding scenarios

scenario (778) despite consuming fewer aphids (3930 for TCvar; 5231 for TCconst). In the 210 ppm N treatment, the TCvar scenario also resulted in higher DEP (548 eggs) while consuming fewer aphids (3742 for TCvar; 4001 for TCconst). Our study shows that optimizing the feeding scenario of H. variegata can significantly increase reproductive success, as demonstrated by the optimization results that led to higher DEP with lower aphid consumption. These findings contribute to a better understanding of the ecological interactions between H. variegata and aphids, and have important implications for the development of effective pest management strategies.

In our study, we used GA solutions to analyze the feeding requirements of female *H. variegata* at three distinct stages of their lifespan (i.e., first 15 days, 15th day of the second, and 15th day of the third) in the TCvar feeding scenario, across three different N treatments. We performed one-way ANOVA analysis on the resulting data and presented the findings in Table 3. The comparison of the average values for three key characteristics—total aphid consumption (TC), total aphid weight (TCw), and daily egg production (DEP or R)—revealed that the 110 ppm nitrogen treatment produced significantly different results compared to the 160 ppm and 210 ppm treatments. In fact, the 160 ppm and 210 ppm treatments outperformed the 110 ppm treatment across all three criteria, indicating the effectiveness of nitrogen treatment. Overall, the results suggest that the 160 ppm nitrogen treatment yielded the best outcomes. These findings warrant further discussion, which we will explore in subsequent sections.

Table 3 Results of ANOVA for GA solutions of total aphid consumption (TC), total aphid weight (TCw), and daily egg production (DEP) in *H. variegata* at three intervals after oviposition, across three nitrogen (N) treatment groups and three stages of their lifespan

Time intervals	Inputs	110 ppm N	160 ppm N	210 ppm N	F	*P* value
First 15 d	TC	41.7 ± 2.4^{b}	64 ± 10.5^{a}	66 ± 7^{a}	50	0.0001
	TCw	15.5 ± 0.9^{c}	23.8 ± 3.9^{b}	27.9 ± 2.9^{a}	73	0.0001
	R	4.9 ± 0.01^{c}	16.2 ± 0.06^{a}	12.7 ± 0.05^{b}	178	0.0001
Second 15 d	TC	43 ± 4.04^{c}	61.9 ± 7.5^{b}	70 ± 5.4^{a}	82	0.0001
	TCw	16 ± 1.5^{b}	23 ± 2.8^{b}	30 ± 2.3^{a}	131	0.0001
	R	5 ± 0.01^{b}	13.6 ± 0.04^{a}	12.2 ± 0.04^{a}	56	0.0001
Third 15 d	TC	36 ± 8.7^{c}	50 ± 7.4^{b}	73.4 ± 0.01^{a}	120	0.0001
	TCw	13.3 ± 3.2^{c}	18.3 ± 2.8^{b}	31 ± 0.01^{a}	197	0.0001
	R	3.34 ± 0.03^{c}	7.7 ± 0.07^{a}	8.2 ± 0^{a}	414	0.0001

Values within rows with different letters were significantly different (± SEM) based on the results of one-way ANOVA followed by Turkey's test ($\alpha = 0.05$)

4 Discussion

Results of the present study showed the qualitative and quantitative nutritional needs of the variegated ladybug, *H. variegata* could be reliably predicted and optimized using SVM and GA, respectively. Accordingly, the prediction of daily nutritional requirements throughout the reproductive lifetime of the beetles showed females feeding on aphids exposed to 160 ppm N fertilization treatments would not only consume greater aphid numbers compared to the 110 ppm treated females, but also have a higher efficient transformation rate (Q_p) equating aphid consumption to DEP. Females in the 160 ppm N group reproduced 65% more than those in the 210 ppm N treatment group and had 29.4% higher rates of DEP while requiring fewer aphid meals.

The "protein leverage" hypothesis indicates that some omnivores eating a low-protein diet will binge eat to gain additional protein stores while ingesting other nutrients [45]. In keeping with this prediction, numerous organisms have been shown to prioritize protein intake under dietary protein restriction [46–48]. Most predatorial organisms on an artificial diet can regulate nutrient intake to maximize fitness [4, 49]. However, on natural diets, not only chemical (nutritional and toxic) composition, but also anti-predator behavior of prey can influence foraging responses and limit potential predation [50–54]. Likewise, the model anticipated the 110 ppm N treated females would be weaker predators compared to those in other treatments as TC of this group was lowest during each of the 15 d intervals (Table 3).

Predators foraging in environmental with low nutritional value food options must strike a balance between maximizing nutrition and energy intake and minimizing predation costs such as high toxicity levels or prey chemical defense. Thus, TC in these circumstances would decrease to prevent accumulation of toxic compounds [6, 55–57]. A similar decreased food intake in response to subpar prey options was observed in two predator spider species of the genus *Pardosa* (Arenae: Lycosidae) [3, 58].

The model revealed all input variables contributed < 50% to DEP within the 110 ppm N group and increased prey availability did not alter beetle feeding habits. Therefore, the beetles instinctively limited prey intake to maximize TE rather than quality. Energy intake is likely the primary currency motivating foraging in suboptimal ecosystems with predators killing at lower rates. Thus, as a consequence, nutrient deficiency (especially protein) may have prevented females from producing high-quality gametes and carbohydrate scarcities lowered male beetle mating and courtship behavior [7, 59]. Beetles subjected to the 110 ppm N treatment had lower reproductive capacities after receiving food so poor in quality their overall nutritional demands were not met limiting energy available for egg production. Optimization of DEP for the 110 ppm N group showed maximum egg production occurred at 21 d compared to 14 d and 18 d for females from the 160 ppm N and 210 ppm N groups.

SVM predicted reproduction rates in the 210 ppm N group was tightly controlled with all nutritional input variables contributing > 80% to DEP and the highest TC rates for each N treatment at three intervals compared to 160 ppm N females at higher prey densities. Beetles living in a high-quality nutritionally abundant environment had elevated metabolic rates and greater body mass [60] as a larger proportion of resources were available for diversion to growth and development [61] compared to beetles from lower quality environments. Thus, beetles from the 210 ppm N group were more voracious and aggressive predators than those from either other group. Increased consumption when prey were numerous led to excessive energy depletion in the 210 ppm N group as females spent

more time foraging and handling prey to maintain their larger body mass, leaving fewer resources for reproduction [49]. Reproduction in this group began later and required more TE than the 160 ppm N group. Similarly, the model showed DEP rates in the 210 ppm N group was heavily dependent on all nutrient variables and TE. Consumption of protein-rich prey led to increased TE demands and an elevated metabolic rate in these predators.

Inversely, several studies involving spiders have indicated that feeding variable nutrient diets would not result in adjusted metabolic rates [62, 63]. Indeed, mature spiders collected from the native environment continued their natural feeding behavior and wasted few nutrients [63]. The model prediction results raised the question as to how predators in controlled systems or naturally present in agricultural systems adjusted their metabolism to suit their nutritional environments. DEP in the 160 ppm N treatment beetles was more sensitive to [P] and [Carb] than TE, which could explain the superior DEP for the group. Thus, energy expenditures for foraging and body maintenance is minimal. As prey density increased, a responding improvement in DEP for the 160 ppm N group was observed despite a lower TC requirement compared to the 210 ppm N group females (Fig. 5). Thus, of the three N treatment groups, the 160 ppm *H. variegata* females most efficiently utilized TE inputs and transformed it into DEP. The GA-optimized *H. variegata* feeding requirements for TCconst indicated, regardless of the treatment type, beetle DEP would decline compared to TCvar (Fig. 7). Beetles lacking prey limitations did not have the highest DEP rates, even during times of peak predator reproduction. Likely Hall et al. [64] reported a less favorable beetle environment may have been presented despite large quantities of readily available prey. It is also possible a larger portion of time was devoted to capturing and digesting prey items rather than courtship and egg production. In contrast, the GA indicated reproduction rates increased and TC decreased for all three N treatments for TCvar compared to TCconst.

Abiotic environment fluctuations need to be considered when mass rearing [65], thus daily consumption under TCconst conditions may reduce predator reproductive rates and increase mass rearing costs as was evidenced in the 210 ppm N treatment when both TCvar and TCconst maintained similar DEP rates during peak reproduction. Jensen et al. [4] showed feeding *Pardosa prativaga* Koch, 1870 (wolf spider) high-quality prey significantly increased its biomass compared to those fed low-quality meals [63]. Further research on TCvar effects on predator fitness is suggested.

5 Conclusion

Overall, our results suggested rearing *H. variegata* with prey fed 210 ppm N was suitable for short-term biological control applications as the beetles are voracious and aggressive predators requiring high levels of energy and nutrition. SVM predicted the macronutrient composition of aphids reared with the 160 ppm N treatment was balanced such that *H. variegata* females utilized them more efficiently for reproduction compared to the other N treatments. Therefore, the 160 ppm N treatment is nearing the target intake [66] for maximization of females *H. variegata* fitness [67, 68]. Also, for long-term (inoculative release) and mass rearing programs where prey abundance varies, the 160 ppm N treatment is suitable because it generated the greatest transformation efficiency (Q_p) from food intake to DEP.

Here, SVM accurately predicted *H. variegata* reproduction rates from nutritional availability data and showed if prey nutrient composition differs from the nutrient demand of its predator, an inefficient biocontrol would result. Predator nutrient optimization is vital for voracious predators and prey rearing is a costly, time consuming, and labor intensive process.

Acknowledgements The authors are grateful to the Ferdowsi University of Mashhad for Grant No. P3/33503 which provided financial support for this research. The authors declare no conflicts of interest.

Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors have declared no conflicts of interest for this article.

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