Nonlinear models for describing development and fecundity of the pseudococcid predators Nephus includens and Nephus bisignatus

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Nonlinear models for describing development and fecundity of the pseudococcid predators *Nephus includens* and *Nephus bisignatus*

**ABSTRACT**

Among several mathematical models used to describe the development or the fecundity of insects the equations of Enkegaard, Analytis, Bieri 1 and Bieri 2 could describe both biological features. In the current study these equations used to describe the development and fecundity of two pseudococcid predators [*Nephus includens* (Kirsch) and *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae)] preying on *Planococcus citri* (Risso) (Hemiptera: Pseudococcidae) at constant temperatures (15°C - 35°C). All models have goodness of fit to data especially for development [$R^2_{adj}$, RSS and AIC ranged 0.9908-0.9996, 0.0019-89.1752 (x10⁻⁴), and (-75.43) – (-31.07) respectively]. Optimum temperature ($T_{opt}$) and upper threshold ($T_{max}$) were calculated accurately by all models ($T_{opt}$ ranged 32.6-34.0°C for *N. includens* and 30.0-30.6°C for *N. bisignatus* and $T_{max}$ ranged 35.0-38.8°C for *N. includens* and 33.1-36.0°C for *N. bisignatus*, respectively). Lower temperature threshold ($T_{min}$) was calculated accurately by Bieri-1 model (11.0 and 10.0°C for *N. includens* and *N. bisignatus* respectively) whereas Analytis model underestimated it (8.0 and 4.9°C). As far as fecundity is concerned the respective values were better fitted near the optimum temperature (25°C) [$R^2_{adj}$, RSS and AIC ranged 0.8246-0.9704, 9.2729-24.0736 and (-246.82) – (-115.34) respectively]. Conclusively, from the tested models the Bieri-1 equation was proved as the most appropriate for the reason that could estimate correctly all the requested parameters concerning the development ($T_{min}$, $T_{opt}$, $T_{max}$) as well as it could describe sufficiently the fecundity trend of the two predators.

**KEYWORDS:** degree- days, development threshold, model, temperature.

**Introduction**

*Nephus bisignatus* (Boheman) and *N. includens* (Kirsch) (Coleoptera: Coccinellidae) are species of the Palearctic region and important indigenous predators of mealybugs (Hemiptera: Pseudococcidae) in Greece (Argyriou et al. 1976, Kontodimas 1997). *Nephus bisignatus* is also reported from Northern Europe (South Norway, Finland, Sweden, Denmark, Netherlands and Germany) (Pope 1973), as well from Morocco, Southern France, Italy and Portugal (Pope1973, Francardi and Covassi 1992, Magro et al. 1999) whereas *Nephus includens* is also found in Southern Europe (Turkey, Italy, Spain and Portugal) (Bodenheimer 1951, Viggiani 1974, Longo and Benfatto 1987, Suzer et al. 1992, Magro et al. 1999). *Nephus bisignatus* is larger in size (1.5-2 mm length and 1.1-1.2 mm width) than *N. includens* (1.5-1.8 mm length

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Detailed research has been carried out concerning the study of the development and the life tables of the two coccinellids (Kontodimas et al. 2004, 2007). The lower temperature thresholds are estimated to be 10.9 and 9.4°C and thermal constants to be 490.5 and 614.3 degree-days for *N. includens* and *N. bisignatus*, respectively, using a linear model. The upper temperature thresholds are estimated to be 36.1 and 34.7°C, respectively, using the Lactin non-linear model (Kontodimas et al. 2004). The average total fecundities of *N. includens* at 15, 20, 25, 30, 32.5 and 35°C were 49.2, 97.8, 162.8, 108.5, 87.4 and 31.1 eggs/female and the intrinsic rates of increase (*r_m*) 0.014, 0.041, 0.083, 0.086, 0.077 and 0.024 females/female/day, respectively. For *N. bisignatus*, the average total fecundities at 15, 20, 25, 30 and 32.5°C were 54.7, 72.1, 96.9, 56.0 and 22.8 eggs/female, and the intrinsic rates of increase (*r_m*) were 0.017, 0.035, 0.060, 0.051 and 0.024 females/female/day, respectively (Kontodimas et al. 2007).

Several mathematical models have been used for describing the development of insects over a wide range of temperatures such as Logan-6, Lactin, Sharpe and DeMichele, Briere, Bieri-1 and 2, Analytis and Enkegaard equations (Lactin et al. 1995, Roy et al. 2002, Kontodimas et al. 2004, Arbab et al. 2006, 2008, Zahiri et al. 2010, Ranjbar et al. 2011). Similarly, some mathematical models have been used to describe fecundity or fertility at different temperatures such as the equations of Bieri-1 and 2, Enkegaard, Ydergaard and Analytis (Bieri et al. 1983, Enkegaard 1993, Ydergaard et al. 1997, Lanzoni et al. 2004, Kontodimas et al. 2007, Ranjbar et al. 2011).

From the above mentioned models the equations of Enkegaard, Analytis, Bieri 1 and Bieri 2 could describe both features (development and fecundity). In the current study these equations were assessed for their fitness to the experimental data using as indices the adjusted coefficient of nonlinear regression ($R^2_{adj}$), the residual sum of square (RSS) and the Akaike information criterion (AIC).

**Materials and Methods**

**Rearing and experimental conditions**

*Nephus bisignatus* and *N. includens* reared in the laboratory under controlled conditions (15, 20, 25, 30, 32.5, and 35°C; 65±2% RH; L:D 16:8h) in incubators (model MLR-3500T, 3500HT; Sanyo). Newly laid eggs were placed individually in plastic petri dishes and transferred to incubators. On hatching, coccinellid larvae were constantly supplied with an excess of *P. citri* of various stages. Progress in development (hatching, pupation, moulting, adult emergence) and survival was assessed every 12h. In case of immature mortality, the dead individual was removed and replaced by another of the same age, taken from laboratory rearing of the same temperature. Thereby, 25 individuals (males and females) of each species completed their development to adult emergence. The pre-ovipositional period (time interval required for ovary maturation and initiation of mature egg production) was measured for newly emerged females (*N* =25) of both species. The total time for completion of the biological cycle (time elapsed from egg stage until adult oviposition) was estimated by adding the duration of immature stages with the respective pre-ovipositional period (Kontodimas et al. 2004). The fecundity of the two predators was determined using 25 newly emerged pairs of adults of each species, which were kept in plastic cages under the above mentioned constant conditions. The longevity and fecundity of the 25 females were recorded daily (Kontodimas et al. 2007).
Non-linear Mathematical Models

Enkegaard Model
This non-linear model was suggested by Enkegaard (1993) to fit fecundity data:
\[ r(T) = \left( a + b \times T \right) \times \left[ e\left( -\left( c + d \times T \right) \right) \right] \]
where \( r(T) \) is the developmental rate or the daily fecundity, \( T \) is temperature or female adult age, depending on fitted data, \( a, b, c \) and \( d \) are empirical constants.

Bieri-1 and Bieri-2 Models
Also these equations were used to fit the data of fecundity (Bieri et al. 1983):

Bieri-1:
\[ r(T) = [a \times (T - x_{\text{max}})] - [b^{(T-x_{\text{max}})}] \]
where \( r(T) \) is developmental rate or fecundity, \( T \) is temperature or adult female age depending on the fitted data, \( x_{\text{max}}, x_{\text{min}}, a, \) and \( b \) are empirical constants (\( x_{\text{max}}, x_{\text{min}} \) represent the lower and upper temperature threshold or the days of starting and stopping of oviposition).

Bieri-2:
\[ r(T) = a \times \frac{(T - x_{\text{min}})}{b^{(T-x_{\text{max}})}} \]
where \( r(T) \) is considered as developmental rate or daily fecundity, \( T \) is temperature for developmental rate or female adult age for daily fecundity, depending on fitted data, \( x_{\text{min}}, a, \) and \( b \) are empirical constants.

Analytis Model
The Analytis model was developed to determine relationship between temperature and developmental time of phytopathogenic fungi and plant pests (Analytis 1980). However this model could also describe the fecundity of insects (Kontodimas et al. 2007). The expression of this model is:
\[ r(T) = a \cdot (T - x_{\text{min}})^m \cdot (x_{\text{max}} - T)^n \]
where \( r(T) \) is developmental rate or fecundity, \( T \) is temperature or adult female age depending on the fitted data and \( x_{\text{max}}, x_{\text{min}}, a, m \) and \( n \) are empirical constants (\( x_{\text{max}}, x_{\text{min}} \) represent the lower and the upper thresholds for development or the first and the final age of oviposition).

All of the non-linear models were assessed for goodness of fit to data based on:
- The adjusted coefficient of non-linear regression (\( R^2_{\text{adj}} \)):
\[ R^2_{\text{adj}} = 1 - \left( \frac{n - 1}{n - p} \right) \cdot (1 - R^2) \]
where \( n \) is the number of observations, \( p \) is the number of model parameters, and \( R^2 \) is the coefficient of non-linear regression. This criterion is parameter independent. Higher value of \( R^2_{\text{adj}} \) indicates better fit.
- The residual sum of square (\( RSS \)): Lower value of \( RSS \) indicates better fit.
- The Akaike information criterion (\( AIC \)): \( AIC = n \cdot \ln(\text{RSS} / n) + 2p \),
where \( n \) is the number of observations and \( p \) the number of model parameters. Lower value of \( AIC \) indicates better fit (Akaike 1974).

The non-linear regressions for the development and fecundity of Nephus inculdens and N. bisignatus were analyzed with the Marquardt algorithm (Marquardt 1963) using the JMP (v. 4.02; SAS Institute 1989) statistical program.

Results and Discussion
Data concerning development and fecundity of the two predators are presented in Table 1. All fitted parameters were estimated by regression analysis, whereas the measurable parameters were calculated by solving the equations or their first derivatives. The parameters and the values of estimated criteria for model evaluation are presented in Tables 2, 3 and 4.

The curves of the influence of temperature on developmental rate of overall immature stages fitted by each model are shown in Fig. 1. The respective curves concerning the fecundities of the two predators are presented in Figs. 2 and 3.
TABLE 1. Development and fecundity (mean ± SE) of the pseudococcid predators *Nephus bisignatus* and *N. includens* at constant temperatures.

| Temperature (°C) | *N. includens* (days) | *N. bisignatus* (days) | *N. includens* (eggs/female) | *N. bisignatus* (eggs/female) |
|------------------|------------------------|------------------------|-----------------------------|-----------------------------|
| 15               | 114.32 ± 1.61          | 112.98 ± 2.51          | 49.2 ± 2.5                  | 54.7 ± 2.6                  |
| 20               | 55.82 ± 1.10           | 58.06 ± 2.90           | 97.8 ± 2.9                  | 72.1 ± 2.4                  |
| 25               | 34.90 ± 0.46           | 38.06 ± 2.25           | 162.8 ± 5.7                 | 96.9 ± 2.5                  |
| 30               | 25.50 ± 0.66           | 30.32 ± 2.14           | 108.5 ± 3.6                 | 56.0 ± 1.6                  |
| 32.5             | 22.80 ± 1.53           | 34.30 ± 1.84           | 87.4 ± 3.2                  | 22.8 ± 1.1                  |
| 35               | 25.84 ± 1.57           | -                      | 31.1 ± 1.5                  |

FIG. 1. Fitting of nonlinear models on development of *Nephus includens* and *N. bisignatus*. In all charts, the ordinate is the rate of development (1/D, in days⁻¹), and the abscissa is the temperature (in °C).
TABLE 2. Fitness of nonlinear models to the development of the pseudococcid predators *Nephus bisignatus* and *N. includens*.

| Model        | Parameters | *N. includens* | *N. bisignatus* |
|--------------|------------|----------------|-----------------|
|               |            |                 |                 |
| Bieri-1      | a      | 0.002046 ± 0.000050 | 0.001744 ± 0.000055 |
|              | b       | 5.183307 ± 9.678861 | 1.945088 ± 0.253437 |
|              | xmin    | 37.769480 ± 3.114961 | 39.408338 ± 1.271350 |
|              | xmax (≈ tmin) | 10.951158 ± 0.310764 | 9.974940 ± 0.325453 |
|              | topt    | 33.7            | 30.5            |
|              | tmax    | 36.0            | 34.7            |
|              | R² adj  | 0.9985         | 0.9988         |
|              | RSS (10⁻⁴) | 0.6044        | 0.1250         |
|              | AIC     | -61.034        | -56.496        |
| Bieri-2      | a      | -0.018947 ± 0.000966 | -0.015074 ± 0.000613 |
|              | b       | 0.850826 ± 0.005341 | 0.845770 ± 0.004176 |
|              | xmin (≈ tmax) | 38.767602 ± 0.387503 | 35.941459 ± 0.264145 |
|              | topt    | 32.6            | 30.1            |
|              | R² adj  | 0.9938         | 0.9966         |
|              | RSS (10⁻⁴) | 3.5663        | 0.6499         |
|              | AIC     | -52.383        | -50.254        |
| Analytis     | a      | 0.000479 ± 0.000268 | 0.000379 ± 0.000000 |
|              | T_min  | 7.960193 ± 1.138093 | 4.912560 ± 0.000021 |
|              | T_max  | 35.027647 ± 0.044579 | 33.078122 ± 0.000188 |
|              | n      | 1.394577 ± 0.148580 | 1.776622 ± 0.000034 |
|              | m      | 0.057720 ± 0.021610 | 0.174076 ± 0.000009 |
|              | topt   | 34.0            | 30.6            |
|              | R² adj  | 0.9995         | 0.9966         |
|              | RSS (10⁻⁴) | 0.0425        | 0.0019         |
|              | AIC     | -74.962        | -75.428        |
| Enkegaard    | a      | 1.936232 ± 0.293853 | 3.340830 ± 0.359428 |
|              | b      | -0.049945 ± 0.007207 | -0.092952 ± 0.009470 |
|              | c      | 7.2320754 ± 0.362901 | 7.839623 ± 0.459907 |
|              | d      | -0.161547 ± 0.006278 | -0.167508 ± 0.004938 |
|              | topt   | 32.6            | 30.0            |
|              | tmax   | 38.8            | 36.0            |
|              | R² adj  | 0.9908         | 0.9932         |
|              | RSS (10⁻⁴) | 89.1572       | 16.2472        |
|              | AIC     | -31.070        | -32.159        |
TABLE 3. Fitness of nonlinear models to data of fecundity of the pseudococcid predator *Nephus includens* at constant temperatures

| Model/Parameters | 15°C | 20°C | 25°C | 30°C | 32.5°C | 35°C |
|------------------|------|------|------|------|--------|------|
| **Analytis**     |      |      |      |      |        |      |
| $a$              | 0.0560x10^{-6} | 0.0699x10^{-9} | 1.5284x10^{-6} | 0.2074x10^{-6} | 0.6510x10^{-7} | 2.2901x10^{-7} |
| $D_{min}$        | $0^{10}$ | 9.5208 | 3.9094 | 5.9629 | 4.6541 | 4.7292 |
| $D_{max}$        | 22.9964 | 127.9999 | 98.8467 | 122.1913 | 106.8212 | 55.3308 |
| $n$              | 211.3905 | 1.3136 | 0.3567 | 0.2460 | 0.6121 | 0.5811 |
| $m_1$            | 0.6832 | 4.3721 | 3.1611 | 3.3878 | 3.4995 | 1.9278 |
| $R^2_{adj}$      | 4.5884 | 0.8957 | 0.9704 | 0.8640 | 0.8170 | 0.7823 |
| $RSS$            | 0.6298 | 14.2759 | 12.8859 | 21.7619 | 15.3284 | 3.9849 |
| $AIC$            | 13.0140 | -239.23 | -170.84 | -110.56 | -106.50 | -112.96 |
|                  | -363.59 |      |      |      |        |      |
| **Bieri-1**      |      |      |      |      |        |      |
| $a$              | -0.0062 | -0.0241 | -0.0598 | -0.0369 | -0.0378 | -0.0363 |
| $b$              | 0.8890 | 0.9051 | 0.6094 | 0.6256 | 0.8252 | 0.8161 |
| $x_{max}$        | 158.1020 | 112.9830 | 80.5844 | 84.2101 | 77.7340 | 50.9418 |
| $x_{min}$        | 19.8986 | 19.5896 | 6.3986 | 7.2743 | 9.5927 | 6.8444 |
| $R^2_{adj}$      | 0.6177 | 0.8207 | 0.9439 | 0.7528 | 0.8058 | 0.7793 |
| $RSS$            | 13.5452 | 24.2148 | 24.0736 | 25.1653 | 15.8350 | 3.9479 |
| $AIC$            | -373.24 | -186.67 | -115.34 | -99.92 | -106.10 | -115.41 |
|                  | -363.59 |      |      |      |        |      |
| **Bieri-2**      |      |      |      |      |        |      |
| $a$              | 0.0834 | 0.2442 | 0.9430 | 0.5471 | 0.3967 | 0.2968 |
| $b$              | 1.0420 | 1.0492 | 1.0794 | 1.0744 | 1.0683 | 1.0984 |
| $x_{min}$        | 21.8056 | 11.1616 | 2.2699 | 3.4707 | 4.1489 | 4.3513 |
| $R^2_{adj}$      | 0.6513 | 0.8740 | 0.9611 | 0.8695 | 0.8347 | 0.7813 |
| $RSS$            | 12.6902 | 18.7506 | 17.1473 | 22.3715 | 14.1230 | 3.9593 |
| $AIC$            | -385.41 | -219.61 | -148.56 | -112.16 | -116.56 | -117.27 |
|                  |      |      |      |      |        |      |
| **Enkegaard**    |      |      |      |      |        |      |
| $a$              | -1.7280 | -1.3964 | -1.0943 | -0.6405 | -0.7247 | -0.5264 |
| $b$              | 0.0792 | 0.1251 | 0.4821 | 0.1845 | 0.1747 | 0.1210 |
| $c$              | -0.9487 | -1.2051 | -0.8442 | -1.3358 | -1.0943 | -1.3057 |
| $d$              | 0.0411 | 0.0480 | 0.0764 | 0.0718 | 0.0661 | 0.0938 |
| $R^2_{adj}$      | 0.6490 | 0.8730 | 0.9606 | 0.8679 | 0.8324 | 0.7765 |
| $RSS$            | 12.6902 | 18.7506 | 17.1473 | 22.3715 | 14.1230 | 3.9593 |
| $AIC$            | -383.41 | -217.61 | -146.56 | -110.16 | -114.56 | -115.27 |
FIG. 2. Fitting of nonlinear models on fecundity data of *Nephus includens*. In all charts, in the ordinate is presented the daily fecundity (eggs laid per female per day) and in the abscissa is presented the longevity of adult females (days after adult females’ emergence).
TABLE 4. Fitness of nonlinear models to data of fecundity of the pseudococcid predator *Nephus bisignatus* at constant temperatures.

| Mode/Parameters | Temperature |
|-----------------|-------------|
|                 | 15°C  | 20°C  | 25°C  | 30°C  | 32.5°C |
| Analytis        |       |       |       |       |        |
| \(a\)           | 0.5800x10^-9 | 0.0235 | 0.7103x10^-11 | 0.0329 | 2.4724x10^-5 |
| \(D_{\text{min}}\) | 25.9349 | 12.5509 | 5.8130 | 5.9842 | 6.0000 |
| \(D_{\text{max}}\) | 199.0866 | 149.9998 | 214.8710 | 98.0000 | 98.9992 |
| \(n\)           | 0.7145  | 0.1611  | 0.2643  | 0.1966  | 0.4378  |
| \(m\)           | 3.3249  | 0.6685  | 4.8863  | 0.6764  | 2.1116  |
| \(R^2_{\text{adj}}\) | 0.8089  | 0.7684  | 0.8827  | 0.7027  | 0.7006  |
| \(RSS\)         | 9.7424  | 7.8320  | 9.7829  | 7.7660  | 3.2617  |
| \(AIC\)         | -487.69 | -409.27 | -239.20 | -224.39 | -200.58 |
| Bieri-1          |       |       |       |       |        |
| \(a\)           | -0.0083 | -0.0095 | -0.0252 | -0.0128 | -0.0138 |
| \(b\)           | 0.9210  | 0.9088  | 0.6882  | 0.8328  | 0.7992  |
| \(x_{\text{max}}\) | 170.1980 | 161.1187 | 105.5711 | 119.5261 | 83.9593 |
| \(x_{\text{min}}\) | 24.2492  | 14.4014  | 7.4009  | 6.9846  | 6.3123  |
| \(R^2_{\text{adj}}\) | 0.7785  | 0.8273  | 0.8246  | 0.7154  | 0.7156  |
| \(RSS\)         | 11.5360 | 6.3982  | 9.2729  | 7.7872  | 3.1634  |
| \(AIC\)         | -460.45 | -440.39 | -246.82 | -226.14 | -204.69 |
| Bieri-2          |       |       |       |       |        |
| \(\alpha\)      | 0.0869  | 0.0891  | 0.2939  | 0.1182  | 0.1290  |
| \(b\)           | 1.0338  | 1.0306  | 1.0497  | 1.0383  | 1.0581  |
| \(x_{\text{min}}\) | 22.3410  | 9.6433  | 0.6491  | 1.3294  | 4.4818  |
| \(R^2_{\text{adj}}\) | 0.8073  | 0.8138  | 0.8520  | 0.6820  | 0.6984  |
| \(RSS\)         | 10.5782 | 6.9187  | 12.3201 | 8.5973  | 3.3656  |
| \(AIC\)         | -477.45 | -431.12 | -218.99 | -218.83 | -202.41 |
| Enkegaard        |       |       |       |       |        |
| \(a\)           | -1.1757 | -0.2232 | -0.0371 | -0.0397 | -0.1957 |
| \(b\)           | 0.0526  | 0.0231  | 0.0572  | 0.0298  | 0.0437  |
| \(c\)           | -1.2453 | -1.6377 | -1.6679 | -1.4264 | -1.3358 |
| \(d\)           | 0.0333  | 0.0301  | 0.0485  | 0.0376  | 0.0564  |
| \(R^2_{\text{adj}}\) | 0.8061  | 0.8125  | 0.8875  | 0.6784  | 0.6937  |
| \(RSS\)         | 10.5782 | 6.9187  | 12.3201 | 8.5973  | 3.3656  |
| \(AIC\)         | -475.45 | -429.12 | -216.99 | -216.83 | -200.41 |
FIG. 3. Fitting of nonlinear models on fecundity data of *Nephus bisignatus*. In all charts, in the ordinate is presented the daily fecundity (eggs laid per female per day) and in the abscissa the longevity of adult females (days after adult females’ emergence).
All models have goodness of fit to data especially for development ($R^2_{adj}$, RSS and AIC ranged 0.9908-0.9996, 0.0019-89.1752 (x10^-4), and (-75.43) – (-31.07) respectively). Optimum temperature ($T_{opt}$) and upper threshold ($T_{max}$) were calculated accurately by all models ($T_{opt}$ ranged 32.6-34.0ºC for N. includens and 30.0-30.6ºC for N. bisignatus and $T_{max}$ ranged 35.0-38.8ºC for N. includens and 33.1-36.0ºC for N. bisignatus, respectively). Lower temperature threshold ($T_{min}$) was calculated accurately by Bieri-1 model (11.0 and 10.0ºC for N. includens and N. bisignatus respectively) whereas Analytis model underestimated it (8.0 and 4.9ºC). Bieri-2 and Enkegaard models do not estimate the lower temperature threshold because are asymptotic to the temperature axis on the left. The results obtained by the current analysis are similar with them obtained by the other common used mathematical models (Logan, Lactin etc.) that had been tested in previous studies (Kontodimas et al. 2004, 2007).

As far as fecundity is concerned the respective values were less fitted. However near the optimum temperature (in 25ºC) the models were better fitted [$R^2_{adj}$, RSS and AIC ranged 0.8246-0.9704, 9.2729-24.0736 and (-246,82) – (-115,34) respectively].

Conclusively, this work described accurately the temperature-dependent development and daily fecundity of Nephus bisignatus and N. includens using non-linear models. The results are in agreement with the origin of the two species, demonstrating that the northern originated species has lower temperature thresholds.

From the tested models the Bieri-1 equation was proved as the most appropriate for the reason that could estimate correctly all the requested parameters ($T_{min}$, $T_{opt}$, $T_{max}$) and could describe sufficiently the fecundity trend of the two predators. In addition, the reciprocal of the $a$ parameter of the Bieri-1 model estimate sufficiently the thermal constant ($K$) that usually is estimated by linear model (for N. includens $1/a$ =488.8 and $K$=490.5 degree days and for N. bisignatus $1/a$ =573.4 and $K$=614.3 degree days). For these reasons the Bieri-1 equation is suggested for the describing of both development and fecundity of the studied insects as well as for testing in other poikilotherms.

References

Akaike, H. 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control AC. 19: 716–723.

Analytis, S. 1980. Obtaining of sub-models for modeling the entire life cycle of a pathogen. Z. Pflanzenker. Pflanzenschutz. 87: 371–382.

Arbab, A., D.C. Kontodimas and A. Sahragard. 2006. Estimating development of Aphis pomi De Geer (Homoptera: Aphididae) using linear and nonlinear models. Environ. Entomol. 35: 1208-15.

Arbab, A., Kontodimas D.C. and M.R. McNeill. 2008. Modeling Embryo Development of Sitona discoideus Gyllenhall (Coleoptera: Curculionidae) under Constant Temperature. Environ. Entomol. 37: 1381-88.

Argyriou, L.C., H.G. Stavraki and P.A. Mourikis. 1976. A list of recorded entomophagous insects of Greece. Benaki Phytopathological Institute, Kifissia, Greece. 73 p.

Bieri, M., J. Baumgartner, G. Bianchi, V. Delucchi and R. von Arx. 1983. Development and fecundity of pea aphid (Acyrtosiphon pisum Harris) as affected by constant temperatures and pea varietes. Mitt. Schweiz. Entomol. Ges. 56: 163-171.

Bodenheimer, F.S. 1951. Citrus Entomology in the Middle East. Uitgeverij Dr. W. Junk Publishers, Gravehenage, The Hague, 663p.

Enkegaard, A. 1993. The poinsettia strain of the cotton whitefly, Bemisia tabaci (Hom.; Aleyrodidae), biological and demographic parameters on poinsettia (Euphorbia

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pulcherrima) in relation to temperature. Bull. Entomol. Res. 83: 535-546.
Francardi, V. and M. Covassi. 1992. Note bio-ecologishe sul Planococcus vovae (Nasonov) dannoso a Juniperus spp. in Toscana (Homoptera: Pseudococcidae). Redia 75: 1-20.
Fürsch, H. 1958. Die mitteleuropaischen Scymnini und deren Verbreitung mit besonderer Berucksichtigung Bayerns (Col. Cocc.). Nachr.bl. Bayer. Entomol. 7: 75-79; 83-91; 100-102.
Kontodimas, D.C. 1997. First record of the predatory insect Nephus bisignatus (Boheman) (Coleoptera: Coccinellidae) in Greece. Ann. Inst. Phytopathol. 18: 61-63.
Kontodimas, D.C., P.A. Eliopoulos, G.J. Stathas and L.P. Economou. 2004. Comparative temperature-dependent development of Nephus includens (Kirsch) and Nephus bisignatus (Boheman) (Coleoptera: Coccinellidae) preying on Planococcus citri (Risso) (Homoptera: Pseudo-coccidae): Evaluation of a linear and various non-linear models using specific criteria. Environ. Entomol. 33: 1–11.
Kontodimas, D.C., P.G. Milonas, G.J. Stathas, L.P. Economou and N.G. Kavallieratos. 2007. Life table parameters of the pseudococcid predators Nephus includens and Nephus bisignatus (Coleoptera: Coccinellidae). Eur. J. Entomol. 104: 407-415.
Lactin, D.J., N.J. Holliday, D.L. Johnson and R. Craigen. 1995. Improved rate model of temperature–dependent development by arthropods. Environ. Entomol. 24: 68 – 75
Lanzoni, A., Accinelli, G., Bazzocchi, G.G. and Burgio, G., 2003. Biological traits and life tables of the exotic Harmonia axyridis compared with Hippodamia variegata, and Adalia bipunctata (Col.: Coccinellidae). J. Appl. Entomol. 128: 298-306.
Longo, S. and Benfatto. 1987. Coleotteri entomofagi presenti sugli agrumi in Italia. Inf. Fitopatol. 37: 21-30.
Magro, A., J. Araujo and J.L. Hemptinne. 1999. Coccinellids (Coleoptera: Coccinellidae) in citrus groves in Portugal: listing and analysis of geographical distribution. Bol. San. Veg. Plagas 25: 335-345.
Marquardt, D.V. 1963. An algorithm for least squares estimation of nonlinear parameters. J. Soc. Ind. Appl. Math. 11: 431-441.
Pope, R.D. 1973. The species of Scymnus (s.str.), Scymnus (Pullus) and Nephus (Col., Coccinellidae) occurring in the British Isles. Entomol. Mon. Mag. 109 (1304/6): 3-39.
Ranjbar Aghdam, H., Y. Fathipour and D.C. Kontodimas. 2011. Evaluation of non-linear models to describe development and fertility of codling moth at constant temperatures. Entom. Hellenica 20: 3-16.
Roy, M., J. Brodeur and C. Cloutier. 2002. Relationship between temperature and developmental rate of Stethorus punctillum (Col.: Coccinellidae) and its prey Tetrany-chus mcduieli (Acarina: Tetranychidae). Environ. Entomol. 31: 177–187.
SAS, Institute. 1989. JMP, a guide to statistical and data analysis, version 4.02. SAS Institute, Cary, NC.
Suzer, T., M. Aytas and R. Yumruktepe. 1992. Chemical experiment on citrus white fly (Dialeurodes citri), citrus red mite (Panonychus citri) and citrus rust mite (Phyllocoptruta oleivora Ashmead) in the Mediterranean region. Zirai Mucadele Arastirma Yilligi 22-23: 61-63.
Viggiani, G. 1974. Recherches sur les cochenilles des agrumes. IOBC/WPRS Bull. 3: 117-120.
Ydergaard, S., A. Enkergaard and H.F. Brødsgaard. 1997. The predatory mite Hypoaspis miles: temperature dependent life table characteristics on a diet of scarid larvae, Bradyis paupera and B. tritici. Entomol. Exp. Appl. 85: 177 – 187.
Zahiri, B., Y. Fathipour, M. Khanjani, S. Moharramipour and M.P. Zalucki. 2010.
Preimaginal development response to constant temperatures in *Hypera postica* (Col.: Curculionidae): Picking the best model. Environ. Entomol. 39: 177-189.

**ΠΕΡΙΛΗΨΗ**

Μεταξύ των μαθηματικών πρότυπων που χρησιμοποιούνται για την περιγραφή της ανάπτυξης και της αναπαραγωγικής ικανότητας των αρπακτικών, οι εξισώσεις των Enkegaard, Αναλυτή, Bieri 1 και Bieri 2 έχουν τη δυνατότητα να περιγράψουν και τα δύο βιολογικά χαρακτηριστικά. Στην παρούσα μελέτη αυτές οι εξισώσεις χρησιμοποιήθηκαν για να περιγράψουν την ανάπτυξη και την αναπαραγωγική ικανότητα δύο αρπακτικών των νευδοκόκκων (*Nephus includens* (Kirsch) και *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae)) και *Planococcus citri* (Risso) (Hemiptera: Pseudococcidae) σε σταθερές θερμοκρασίες (15°C - 35°C)?. Όλες οι εξισώσεις είχαν καλή προσαρμογή στα δεδομένα. Ειδικά για την ανάπτυξη των ατελών σταθερών η προσαρμογή έγινε με καλή προσαρμογή στα δεδομένα του Ακαικ (AIC) κυμάνθηκε από 0,9908-0,9996, 0,0019-89,1752 (x10^-3), και (-75,43) – (-31,07), αντίστοιχα. Η ειδική θερμοκρασιακή ανάπτυξης (*Tadj*) και το ανώτερο θερμοκρασιακό όριο (*Tmax*) υπολογίστηκαν ικανοποιητικά από όλες τις εξισώσεις. Η *Tadj* κυμάνθηκε από 32,6-34,0°C για το *N. includens* και από 30,0-30,6°C για το *N. bisignatus*. Η *Tmax* κυμάνθηκε από 35,0-38,8°C για το *N. includens* και από 33,1-36,0°C για το *N. bisignatus*. Το κατώτερο θερμοκρασιακό όριο (*Tmin*) υπολογίστηκε ικανοποιητικά από την εξίσωση Bieri-1 (11,0 και 10,6°C για το *N. includens* και για το *N. bisignatus* αντίστοιχα) ενώ υποκτήθηκε από την εξίσωση Αναλυτή (8,0 και 4,9°C). Στα δεδομένα της γνωστήτερης υπήρξε καλύτερη προσαρμογή στα δεδομένα που αποκτήθηκαν στους 25°C, δηλαδή κοντά στην ειδική θερμοκρασιακή ανάπτυξης [*όταν R^2, R^2_adj, RSS και AIC κυμάνθηκαν από 0,8246-0,9704, 9,2729-24,0736 και (-246,82) – (-115,34), αντίστοιχα*]. Συμπερασματικά, διαπιστώθηκε ότι, από τα μήγα μαθηματικά πρότυπα που δοκιμάστηκαν, η εξίσωση Bieri-1 είναι η πιο κατάλληλη διότι μπορεί να υπολογίσει σωστά όλες τις ζητούμενες παραμέτρους (*Tmin, Tadj, Tmax*) που αφορούν στην ανάπτυξη καθώς και να περιγράφει με ακρίβεια τη μεταβολή της ημερήσιας αναπαραγωγικής ικανότητας των δυο αρπακτικών.