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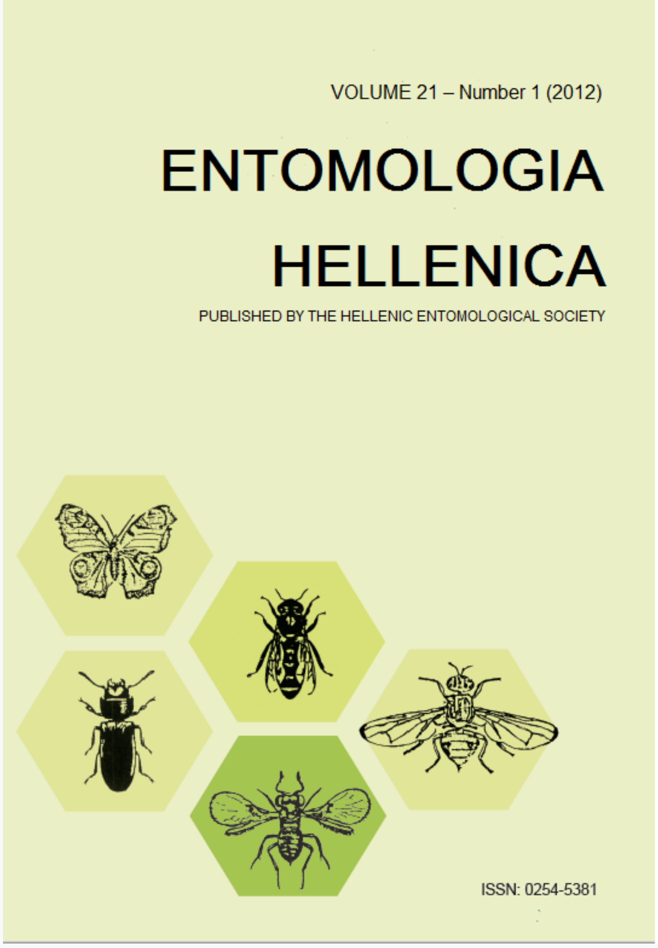

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Nonlinear models for describing development and fecundity of the pseudococcid predators *Nephus includens* and *Nephus bisignatus*

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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 and 1.0-1.1 mm width) (Fürsch 1958, Kontodimas 1997).

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 us 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:

$$r(T) = \left[a \times \left(T - x_{\max}\right)\right] - \left[b^{(T - x_{\min})}\right]$$

where *r(T)* is developmental rate or fecundity, *T* is temperature or adult female age depending on the fitted data, x_{max}, x_{min}, *a,* and *b* are empirical constants (x_{max}, x_{min} represent the lower and upper temperature threshold or the days of starting and stopping of oviposition).

Bieri-2:

$$r(T) = a \times \frac{(T - x_{\min})}{b^{(T - x_{\min})}}$$

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_{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:

$$r(T) = a \cdot (T - x_{min})^n \cdot (x_{max} - T)^m$$

where *r(T)* is developmental rate or fecundity, *T* is temperature or adult female age depending on the fitted data and x_{max}, x_{min}, *a, m* and *n* are empirical constants (x_{max}, x_{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_{adj}):

$$R^2_{adj} = 1 - \frac{(n-1)}{(n-p)} \cdot (1 - R^2),$$

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_{adj} indicates better fit.

- The residual sum of square (*RSS*): Lower value of *RSS* indicates better fit.

- The Akaike information criterion (*AIC*): $AIC = n \cdot \ln(RSS\ /\ n) + 2p$,

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 includens* 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	

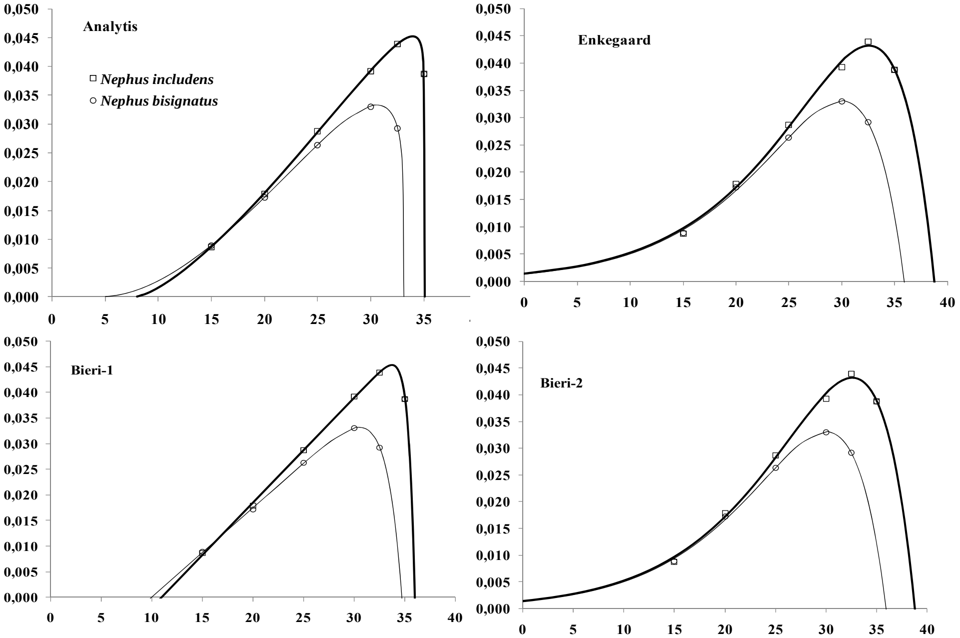

FIG. 1. Fitting of nonlinear models on development of *Nephus includens* and *N. bisignatus*. In all charts, the ordinate is the rate of development (1/D, in days^{-1}), and the abscissa is the temperature (in °C).

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
	x_{min}	37.769480 ± 3.114961	39.408338 ± 1.271350
	x_{max} ($\approx t_{min}$)	10.951158 ± 0.310764	9.974940 ± 0.325453
	t_{opt}	33.7	30.5
	t_{max}	36.0	34.7
	R^2_{adj}	0.9985	0.9988
	RSS (10^{-4})	0.6044	0.1250
	AIC	-61.034	-56.496
Bieri-2	α	-0.018947 ± 0.000966	-0.015074 ± 0.000613
	b	0.850826 ± 0.005341	0.845770 ± 0.004176
	x_{min} ($\approx t_{max}$)	38.767602 ± 0.387503	35.941459 ± 0.264145
	t_{opt}	32.6	30.1
	R^2_{adj}	0.9938	0.9966
	RSS (10^{-4})	3.5663	0.6499
	AIC	-52.383	-50.254
Analytis	a	0.000479 ± 0.000268	0.000089 ± 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
	t_{opt}	34.0	30.6
	R^2_{adj}	0.9995	0.9996
	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
	t_{opt}	32.6	30.0
	t_{max}	38.8	36.0
	R^2_{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	Temperature					
	15°C	20°C	25°C	30°C	32.5°C	35°C
Analytis						
a	0.0560x1	$0.0699x10^{-9}$	$1.5284x10^{-6}$	$0.2074x10^{-6}$	$0.6510x10^{-7}$	$2.2901x10^{-7}$
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	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
Bieri-2						
α	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

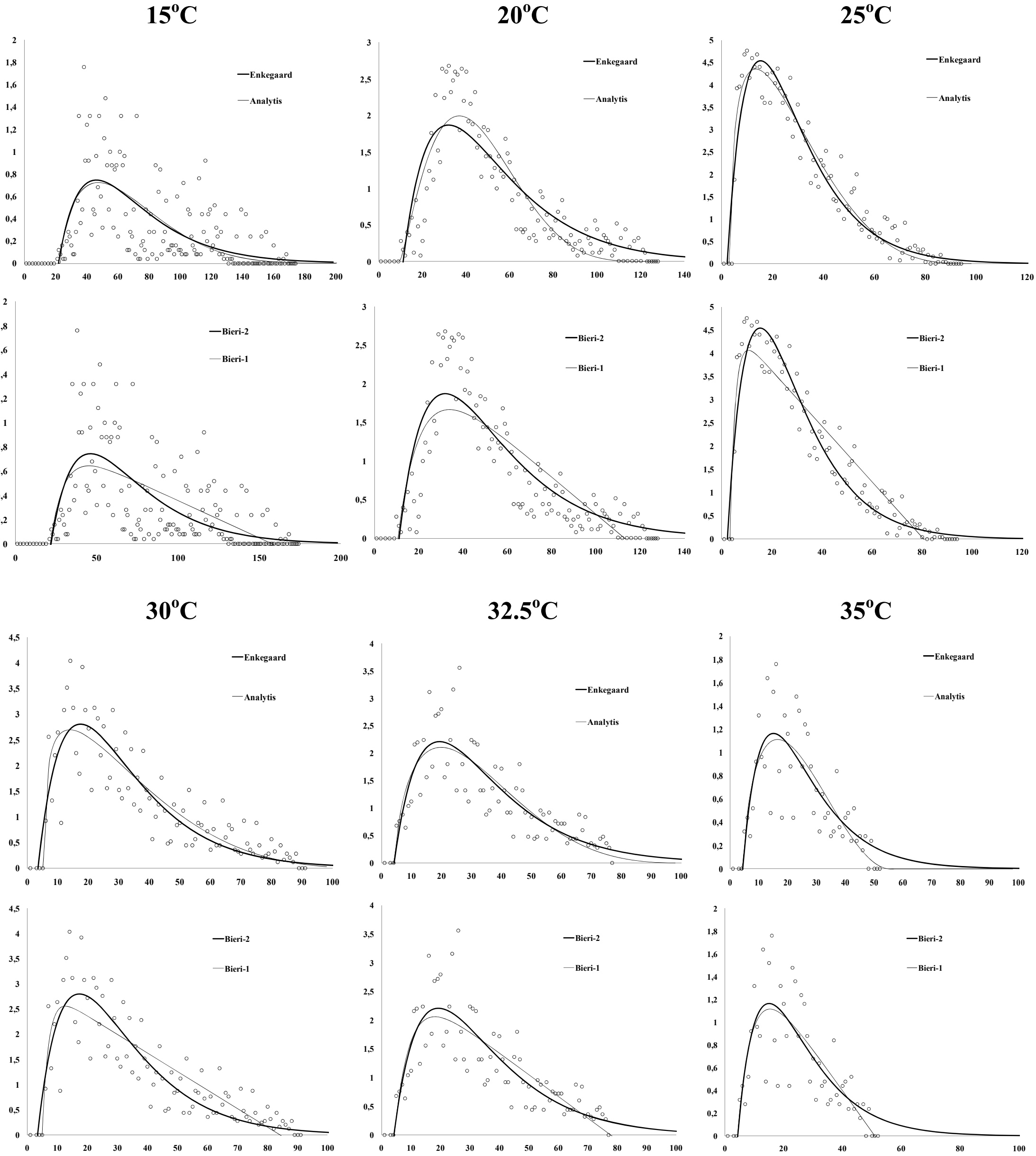

FIG. 2. Fitting of nonlinear models on fecundity data of *Nephus includens*. In all charts, in the ordinate is presented the daily fecundity (eggs laid per female per day) and in the abscissa is presented the longevity of adult females (days after adult females' emergence).

TABLE 4. Fitness of nonlinear models to data of fecundity of the pseudococcid predator *Nephus bisignatus* at constant temperatures.

Mode/ Para-meters	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_{min}	25.9349	12.5509	5.8130	5.9842	6.0000
D_{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_{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_{max}	170.1980	161.1187	105.5711	119.5261	83.9593
x_{min}	24.2492	14.4014	7.4009	6.9846	6.3123
R^2_{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					
α	0.0869	0.0891	0.2939	0.1182	0.1290
b	1.0338	1.0306	1.0497	1.0383	1.0581
x_{min}	22.3410	9.6433	0.6491	1.3294	4.4818
R^2_{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_{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

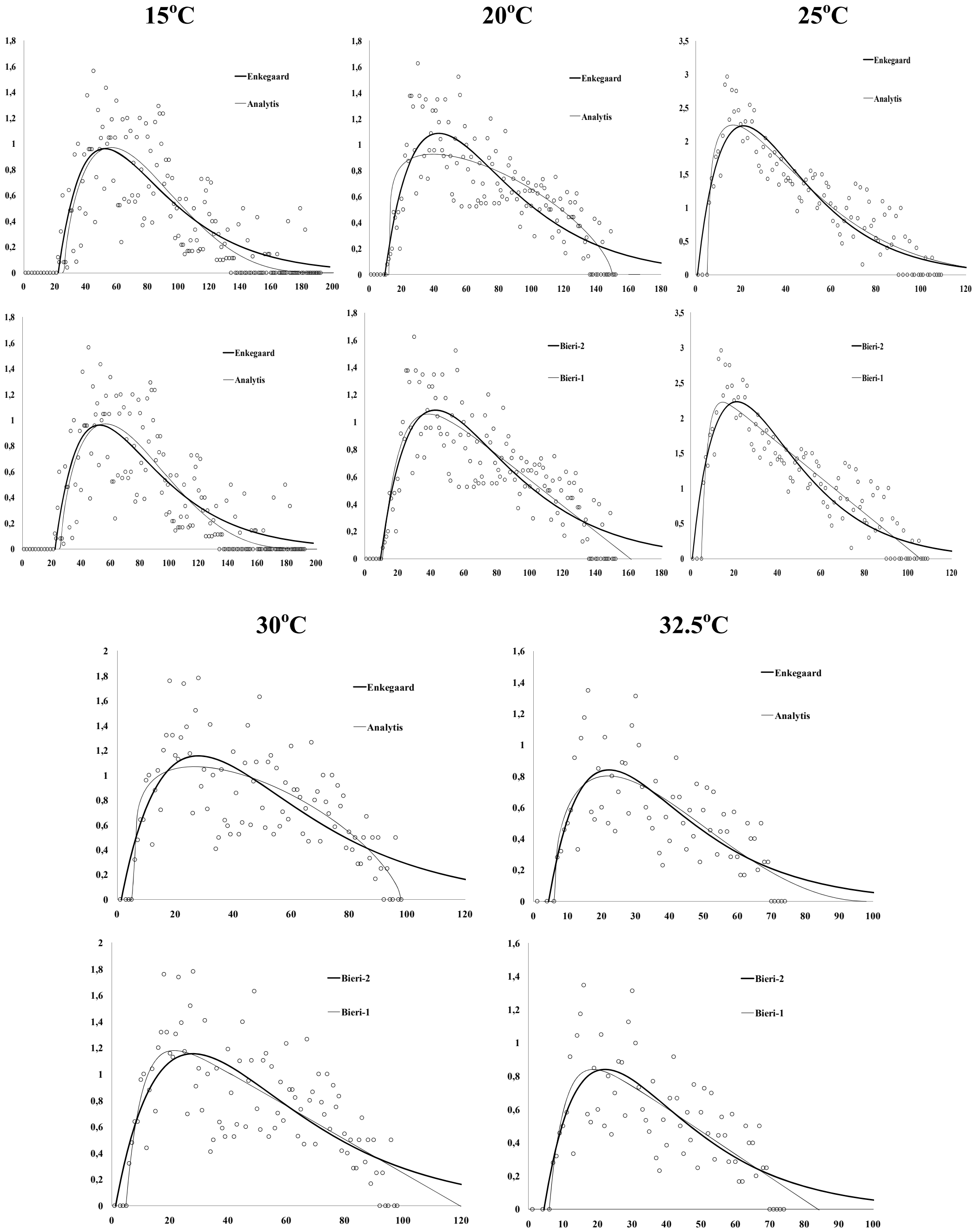

FIG. 3. Fitting of nonlinear models on fecundity data of *Nephus bisignatus*. In all charts, in the ordinate is presented the daily fecundity (eggs laid per female per day) and in the abscissa the longevity of adult females (days after adult females' emergence).

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 32.6-34.0°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). 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 25°C) 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, demonstating 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.

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Μη γραμμικά μαθηματικά πρότυπα για την περιγραφή της ανάπτυξης και της αναπαραγωγικής ικανότητας των αρπακτικών των ψευδοκκόκων *Nephus includens* και *Nephus bisignatus*

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ΠΕΡΙΛΗΨΗ

Μεταξύ των μαθηματικών πρότυπα που χρησιμοποιούνται για την περιγραφή της ανάπτυξης και της αναπαραγωγικής ικανότητας των εντόμων, 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 ψευδοκόκκων [*Nephus includens* (Kirsch) και *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae)] επί *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 σταδίων ο προσαρμοσμένος συντελεστής προσδιορισμού (R^2_{adj}), το άθροισμα τετραγώνων του υπολοίπου (*RSS*) και το πληροφοριακό κριτήριο του Akaike (*AIC*) κυμάνθηκαν από 0,9908-0,9996, 0,0019-89,1752 (x10^{-4}), και (-75,43) – (-31,07), αντίστοιχα. Η ιδανική θερμοκρασία ανάπτυξης (T_{opt}) και το ανώτερο θερμοκρασιακό όριο (T_{max}) υπολογίστηκαν ικανοποιητικά από όλες τις εξισώσεις. Η T_{opt} κυμάνθηκε από 32,6-34,0°C για το *N. includens* και από 30,0-30,6°C για το *N. bisignatus*. Η T_{max} 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 (T_{min}) υπολογίστηκε ικανοποιητικά από την εξίσωση Bieri-1 (11,0 και 10,0°C για το *N. includens* και για το *N. bisignatus* αντίστοιχα) ενώ υποεκτιμήθηκε από την εξίσωση Αναλυτή (8,0 και 4,9°C). Στα δεδομένα της γονιμότητας υπήρξε καλύτερη προσαρμογή στα δεδομένα που αποκτήθηκαν στους 25°C, δηλαδή κοντά στην ιδανική θερμοκρασία ανάπτυξης [όπου 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 μη γραμμικά μαθηματικά πρότυπα που δοκιμάστηκαν, η εξίσωση Bieri-1 είναι η πιο κατάλληλη διότι μπορεί να υπολογίσει σωστά όλες τις ζητούμενες παραμέτρους (T_{min}, T_{opt}, T_{max}) που αφορούν στην ανάπτυξη καθώς και να περιγράψει με ακρίβεια τη μεταβολή της ημερήσιας αναπαραγωγικής ικανότητας των δύο αρπακτικών.