

Temperature-dependent development of dubas bug, *Ommatissus lybicus* (Hemiptera: Tropiduchidae), an endemic pest of date palm, *Phoenix dactylifera*

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Abstract. Dubas bug, *Ommatissus lybicus* Bergevin, is an important pest of date palm on the Arab peninsula. This sucking insect causes great damage to the trees and reduces the quantity and quality of the dates. Effect of temperature on the development of the immature stages of *O. lybicus* was studied in the laboratory by rearing them at nine constant temperatures, ranging from 15 to 35°C. Development was successfully completed at temperatures ranging from 20 to 35°C for eggs and from 20 to 32.5°C for nymphs. The lower thermal thresholds for development of eggs, nymphs and egg-adult were estimated by means of linear regression as 12.9, 12.9 and 13.2°C, respectively. Thermal units required for the development of the same stages were 572.5, 648.2 and 1184.4 degree-days, respectively. The lethal high temperatures were also estimated using a nonlinear model as 34.5, 43.4 and 34.6°C for eggs, nymphs and total immature stages, respectively. The development rate and survival data indicate that the optimum temperature range for *O. lybicus* is 25–27.5°C.

INTRODUCTION

Ommatissus lybicus Bergevin, 1930 is known as “dubas” in Arab countries, and “dubas bug” or “old world date bug” in the literature (Kranz et al., 1978). The adult is yellowish brown, to greenish, and the females distinguished by a strongly toothed-saw like ovipositor and are usually longer than the males, reaching 5–6 mm compared to the 3–3.5 mm of males. There are two black spots on the front of the head of both sexes. The egg is elongate in shape, 0.5 to 0.8 mm long and light green in colour when laid, but turns yellowish white, then bright yellow before hatching. There is a distinct suture at the front end of each egg. Most of the egg body is embedded in plant tissue. There are five nymphal instars, each of which is yellow to greenish yellow, distinguished by a bundle of waxy caudal filaments and a number of dorsal grey lines along their bodies (Al-Abbassi, 1988). This species is the most common pest of date palm and widely distributed in Oman. It is recorded in many Arab countries, North Africa, Iran, and Spain, where it causes serious damage to date palms (El Haidari & Al Hafidh, 1986; Walker & Pittaway, 1987; Kinawy, 2005).

This sap sucking species is restricted to date palm *Phoenix dactylifera* L., on which it completes two generations per annum (autumn and spring generations) feeding on the leaves (Hussain, 1985; Howard et al., 2001). Abd-Allah et al. (1998) report that the total nymphal development of the spring generation lasts from 45 to 52 days with an average of 48.4 days. The life span of the adult stage is 82 days for the male and 72 for the female, during which a female can lay up to 143 eggs. Incubation period of the eggs averaged 120 days for the spring generation, and 95 days for the autumn generation.

Despite the importance of *O. lybicus* little is known about the effect of temperature on its phenology. A knowledge of the lower threshold and thermal units required for development are needed to determine the development rate of a particular species of arthropod (Trudgill et al., 2005; Barteková & Praslička, 2006). This study was designed to investigate the effect of temperature on the developmental rate and survival of *O. lybicus* in

order to provide a reliable temperature-driven tool for forecasting and developing better management strategies for this important pest.

MATERIAL AND METHODS

Insect and plant material

Adults of *O. lybicus* were collected from a date palm farm near Bahla (N22°65'25.3; E57°16'12.6), in the interior of Oman. The insects were kept and cultured on date palm seedlings in the laboratory at room temperature, which ranged between 25 and 27°C. The studies were conducted on the F2 of the laboratory-reared insects. Newly emerged adults were collected and kept on date palm seedlings (7 months old) planted in plastic pots (15 cm diameter) covered with cylindrical transparent cages (14 cm diam. × 35 cm high). Twenty adults (10 females and 10 males) were kept on each date palm seedling, with 5 replicates at each temperature tested, under a 14L : 10D light regime. The adults were left for 24 h to lay eggs on the seedling, and then removed so that all the eggs were one day old. The number of eggs laid on each seedling was counted and then the seedling plus eggs were kept at a constant temperature until the eggs hatched. The seedlings were watered by placing the pots in a plastic tray containing water that was taken up by the roots of the seedling through holes at the base of the pots. Then the tray was removed in order to avoid increasing humidity.

Temperature-dependent development

Effect of ambient temperature on the development of immature stages (egg and 5 nymphal instars) of *O. lybicus* was determined at nine constant temperatures: 15, 17.5, 20, 22.5, 25, 27.5, 30, 32.5 and 35°C. The insects were reared on date palm seedlings following the method used for this species by Mokhtar et al. (2003). Sanyo Cooling Incubators provided with white fluorescent lighting were used for this study. The temperatures were mostly controlled within the acceptable accuracy of ±

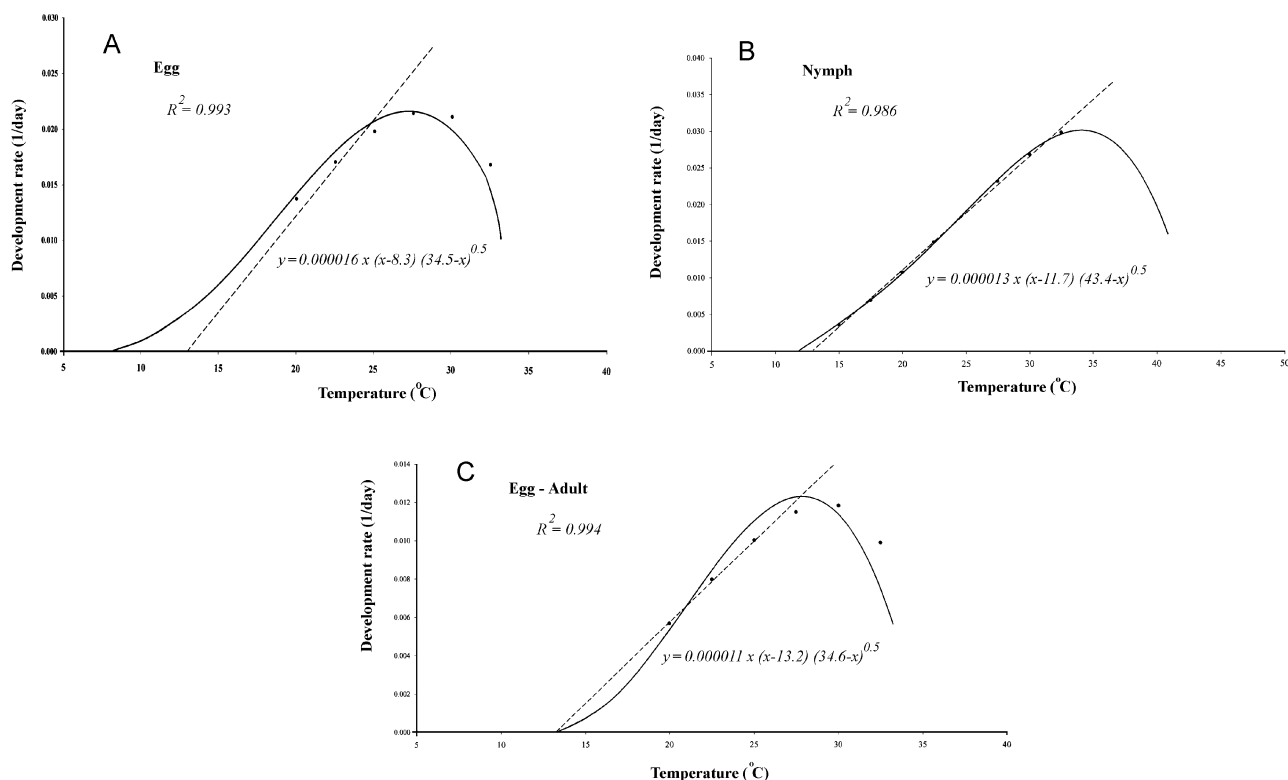


Fig. 1. Influence of temperature on developmental rate of different life stages of *Ommatissus lybicus*. A – egg, B – nymph, C – egg-adult. Dashed line is the relationship predicted by the linear regression and solid line the nonlinear regression curve. The linear regression coefficient (R^2) is at top left of the figure. The equation for the nonlinear model is written under the curve, in which y is the predicted developmental rate and x the given temperature ($^{\circ}\text{C}$).

0.5 $^{\circ}\text{C}$ and RH% ranged between 55 to 65% throughout the study.

The seedlings were inspected at daily intervals to determine the time of egg hatch and the site of each hatched egg was immediately marked using a coloured marker pen. The newly hatched nymphs were immediately transferred to a fresh seedling and assigned to a specified temperature treatment (replicated 5 times, with at least 5 nymphs in each replicate). The nymphs were left to feed and develop on the leaflets of the seedling, monitored daily and the number of moults recorded. The exuviae (cast skins) were counted and then removed carefully without disturbing the nymphs, which if disturbed jump off seedlings.

Developmental times (Dt) were calculated from the date of egg laying to egg hatch, from egg hatch to the first moult and then between each subsequent moult for each nymphal instar. The developmental rates (Dr or days^{-1}) were calculated as reciprocals of development time ($Dr = 1/Dt$).

Survival

Stage-specific survival was calculated for each temperature by dividing the number of individuals alive at the end by the number at the beginning of each stage. The mortality of nymphs was recorded every day and survival calculated for each nymphal instar.

Statistics

Means of the developmental times at different temperatures were analyzed by analysis of variance (ANOVA) and Duncan's multiple range test, using Genstat (Software for Statistical Analysis, 10th ed., VSV International Ltd.).

The linear relation between developmental rate and temperature were described by the following regression model:

$$y = a + bx \quad (1)$$

where y is the developmental rate, x is the given temperature, a and b are the regression parameters. The lower threshold temperature for development (T_{lower}) was calculated using the following equation (Liu & Meng, 1999):

$$T_{\text{lower}} = -a/b \quad (2)$$

The required thermal units (degree-days) for the development (DD) of eggs and nymphs were calculated using the formula:

$$DD = Dt (x - T_{\text{lower}}) = 1/b \quad (3)$$

where Dt is the developmental time in days at temperature x ($^{\circ}\text{C}$) and b is the regression coefficient (Arnold, 1959, 1960; Madubunyi & Koehler, 1974; Liu & Meng, 1999).

The nonlinear function proposed by Briere et al. (1999) was also used to describe the relationship between the developmental rate and temperature over the range 20–35 $^{\circ}\text{C}$ for eggs and 20–32.5 $^{\circ}\text{C}$ for nymphs. The mathematical expression of this model is:

$$y = a x (x - T_{\text{lower}}) \sqrt{(T_{\text{lethal}} - x)} \quad (4)$$

where y is the developmental rate; x is the given temperature ($^{\circ}\text{C}$) and T_{lethal} is the lethal temperature and c a constant. The estimates of the model's parameters for linear and nonlinear regression models were obtained using Gosa-fit (version 3, Bio-Log Scientific software).

RESULTS

Temperature-dependent development

Eggs

Embryos successfully completed their development at temperatures between 20–35 $^{\circ}\text{C}$, but not at temperatures below 20 $^{\circ}\text{C}$. Time (Dt) required for eggs to hatch significantly decreased with increasing temperature from 20 to 27.5 $^{\circ}\text{C}$ ($P <$

TABLE 1. Mean developmental time of eggs and nymphs of *Ommatissus lybicus* at different constant temperatures.

Temperature °C	Developmental time (days ± sd)							
	Egg	Nymph instars					Total nymph stage	Egg-Adult
		N1	N2	N3	N4	N5		
20	80.6 ± 1.34 b	21.0 ± 0.26 a	14.3 ± 1.04 a	14.1 ± 0.64 a	20.7 ± 0.26 a	24.4 ± 0.59 a	94.5 ± 1.23 a	175.1 ± 1.91 a
22.5	60.0 ± 1.22 d	13.2 ± 0.52 b	10.8 ± 0.55 b	12.1 ± 0.36 b	15.6 ± 0.18 b	18.1 ± 0.83 b	69.7 ± 1.08 b	129.7 ± 1.84 b
25	47.6 ± 1.30 f	10.3 ± 0.39 c	7.0 ± 1.05 c	7.4 ± 0.35 c	11.8 ± 0.33 c	14.0 ± 0.72 c	50.4 ± 1.28 c	98.0 ± 1.31 c
27.5	39.2 ± 0.84 g	8.2 ± 0.49 d	6.5 ± 0.10 cd	7.2 ± 0.67 c	9.9 ± 0.30 d	12.9 ± 1.00 d	44.7 ± 0.41 d	83.9 ± 0.70 e
30	50.8 ± 1.30 e	7.0 ± 0.37 e	6.2 ± 0.57 cd	6.7 ± 0.68 c	8.4 ± 0.14 e	9.1 ± 0.76 e	37.6 ± 1.47 e	88.4 ± 2.50 d
32.5	66.0 ± 1.22 c	6.7 ± 0.25 e	5.5 ± 0.75 e	5.9 ± 0.53 d	7.0 ± 0.31 f	8.6 ± 0.82 e	33.7 ± 0.90 f	99.7 ± 0.82 c
35	99.1 ± 0.74 a	—	—	—	—	—	—	—

Means followed by different letters within each column are significantly different (Duncan's multiple range following ANOVA, $P < 0.05$). N – nymphal instar from first to fifth instar; — : no nymphs survived.

TABLE 2. Developmental parameters of eggs and nymphs of *Ommatissus lybicus* estimated using linear regression.

Developmental stage	Regression equation*	R^2	Thermal units (DD)	Thermal threshold (°C) (T_{lower})
Eggs	$y = -0.0226 + 0.0018 x$	0.993	572.5	12.9
(Nymphs) N1	$y = -0.1138 + 0.0084 x$	0.959	119.6	13.6
N2	$y = -0.1006 + 0.0089 x$	0.825	111.4	11.2
N3	$y = -0.0853 + 0.0080 x$	0.847	125.0	10.7
N4	$y = -0.1032 + 0.0075 x$	0.988	133.4	13.8
N5	$y = -0.0868 + 0.0063 x$	0.924	158.4	13.7
Total nymph stage	$y = -0.0199 + 0.0015 x$	0.986	648.2	12.9
Egg-Adult	$y = -0.0112 + 0.0008 x$	0.994	1184.4	13.2

* – using results of 20–27.5°C for eggs and 20–32.5°C for nymphs; N – nymphal instar from first to fifth instars; DD – thermal units above lower temperature threshold; T_{lower} – lower temperature threshold.

0.001). At temperatures higher than 27.5°C, the developmental time increased with increase in temperature. The shortest developmental time (39.2 days) was recorded at 27.5°C and the longest (99.1 days) at 35°C (Table 1). Developmental time of eggs was inversely related to temperatures within the range 20 to 27.5°C, thereafter, it increased at 30°C and higher.

The relationship between the developmental rate of eggs and temperature was described by both linear and nonlinear models (Fig. 1A). Development rate of eggs within the mid-range of 20–27.5°C, was a positive linear function of temperature ($F = 2597.4$, $df = 1, 18$, $P < 0.001$). The lower thermal threshold and thermal units required for development of eggs (equations 2 and 3) a 12.9°C and 572.5 DD above 12.9°C, respectively (Table 2). Plots of the fitted nonlinear model and the recorded rates of development of the eggs at temperatures over the range 20–35°C are shown in Fig. 1 and the parameter estimates are presented in Table 3. The lower temperature threshold for development and high lethal temperature for eggs were estimated using Briere nonlinear model as 8.3 and 34.5°C, respectively.

Nymphs

The trend in the developmental time of the nymphal stage was similar to that recorded for the egg stage between 20 and 32.5°C ($P < 0.001$), with no nymphs surviving at 35°C. The time taken

to complete nymphal development was shortest (33.7 days) at 32.5°C and longest (94.5 days) at 20°C (Table 1).

The developmental rate of the nymphs was a positive linear function of temperature over the range 20 to 32.2°C ($F = 1929.7$; $df = 1, 28$; $P < 0.001$) (Fig. 1B). The linear model indicates that the lower temperature threshold for nymphal development is 12.9°C, and its required thermal units are 648.2 DD. The developmental parameters for each nymphal instar were also estimated (Table 2). Briere's nonlinear model was used to estimate the lower and lethal high temperature thresholds, which are 11.7 and 43.4°C, respectively (Table 3).

Egg-Adult

The total developmental time from egg to adult is a function of embryonic and nymphal development times. Developmental time was significantly different at different temperatures ($P < 0.001$), with the longest and shortest time of 175.1 and 83.9 days at 20 and 27.5°C, respectively (Table 1). A linear regression was fitted to the developmental rate versus temperature results over the mid-range of temperatures, i.e., 20–27.5°C ($F =$

TABLE 3. Parameter estimates for nonlinear model describing the relationship between temperature and developmental rates of immature stages of *Ommatissus lybicus*.

Parameter	Stage		
	Egg	Nymph	Egg-Adult
a	16×10^{-6}	13×10^{-6}	11×10^{-6}
T_{lower}	8.3	11.7	13.2
T_{lethal}	34.5	43.4	34.6
R^2	0.919	0.994	0.987

TABLE 4. Stage-specific survival of *Ommatissus lybicus* at different constant temperatures.

Temperature °C	Survival rate (%)	
	Egg	Nymph
20	19.7 (114) c	23.3 (22) c
22.5	73.0 (744) b	26.4 (89) c
25	85.8 (555) a	78.4 (106) a
27.5	87.1 (1004) a	69.2 (80) ab
30	21.7 (221) c	47.6 (39) bc
32.5	17.9 (554) c	40.1 (76) c
35	17.5 (706) c	—

Means followed by different letters in the same column are significantly different (Duncan's multiple range following ANOVA, $P < 0.05$).

TABLE 5. Instar-specific survival of *Ommatissus lybicus* nymphs reared at different constant temperatures.

Instar	Survival %
N1	61.4 c
N2	86.8 b
N3	98.4 a
N4	96.4 a
N5	94.8 ab
Total nymphal stage	47.5 d

Means followed by different letters in the same column are significantly different (Duncan's multiple range following ANOVA, $P < 0.05$). N – nymphal instar from first to fifth instar.

2943.1, $df = 1, 18$, $P < 0.001$) (Fig. 1C). The lower developmental threshold and number of degree-days required for egg-adult development were calculated as 13.2°C and 1184.4 DD, respectively (Table 2). Nonlinear regression indicated a lower development threshold and lethal high temperature for total immature development of 13.2 and 34.6°C, respectively (Table 3).

Survival

Survival of eggs was significantly affected by temperature ($F = 372.2$; $df = 6, 14$; $P < 0.001$). Survival was highest at 25 and 27.5°C, and lower at 20, 30, 32.5 and 35°C (Table 4).

Survival of nymphs was highest at 25 and 27.5°C and lower at 20, 22.5 and 32.5°C, with no nymphs surviving at 35°C ($F = 8.47$; $df = 5, 24$; $P < 0.001$) (Table 4). The survival of the different nymphal instars differed significantly ($F = 61.6$; $df = 5, 144$; $P < 0.001$). The lowest survival was recorded for the first instar with the later nymphal instars surviving better (Table. 5).

DISCUSSION

The developmental rates of insects, which are poikilotherms, mainly depend on temperature (Dent & Walton, 1997). The developmental rate of the immature stages of *O. lybicus* increased up to an optimum temperature above which it decreased. Eggs of *O. lybicus* hatched at 35°C but nymphs reared at this temperature died shortly after hatching. This may be because most of each egg is embedded and surrounded by live plant tissue, which provides the egg with a more favourable microclimate. Therefore, ambient conditions experienced by eggs and nymphs differ, which may explain why they responded differently to temperature. Moreover, this result indicates that further studies are needed to determine the temperature over the range of 32.5 and 35°C at which the nymphs are at their upper physiological limit.

There are few studies on the effect of temperature on the development time of *O. lybicus*. One reports total developmental time for nymphs of 43.0 and 34.8 days at 27.7 and 30.5°C, respectively (Elwan & Al-Tamimi, 1999). In the present study the total nymphal periods were 44.7 and 37.6 days, respectively at the temperatures cited in the above report. The difference could be due to the temperature cycling (in the cited report) and constant (in the present study) (Jervis, 2007).

Published data on the effect of temperature on the developmental rate of *O. lybicus* collected in Iraq, indicate that the lower developmental thresholds 13.0 and 13.5°C, and the required thermal units 641.0 and 515.6 DD for eggs and nymphs, respectively (Hasson, 1988). The values for lower developmental threshold are similar to that obtained (12.9°C) in this study. In contrast, the required thermal units reported by Hasson (1988) differ. However, geographically separated popu-

lations of the same species may differ genetically and biologically (Honěk, 1996; Tang et al., 1999). In addition, if the parents of the eggs used in different studies are reared at different temperatures then that could also affect the results.

In the present study linear and nonlinear models were used to describe the relation between the developmental rate of *O. lybicus* and temperature. A linear model was used to determine the relationship over the mid range of temperatures as within this range the relationship is linear. Overall, however, the relationship between the rate of development and temperature is nonlinear at the extremes of an insect's physiological tolerance (Logan et al., 1976; Brady & Lyonns, 2003; Diaz et al., 2007). The calculated lower thermal thresholds for development of eggs and nymphs is lower than the lowest temperature at which development was recorded (Fig. 1). This was probably due to using a linear equation to describe a nonlinear relationship between temperature and developmental rate (Wagner et al., 1984).

The developmental parameters and survival at all the temperatures tested indicate that the optimum temperature range for the immature stages of *O. lybicus* is 25–27.5°C. The high mortality recorded when reared at temperatures outside this range indicates that these temperatures have an inhibitory effect on development. This explains why the post embryonic stages of *O. lybicus* are abundant in the field in Oman in February–March and September–October, when the temperature is within the optimum range.

This study is the first stage in an attempt to determine how the phenology of a widely geographically distributed species, *O. lybicus*, is synchronized with local climatic conditions. Degree-day calculations can be used to develop phenology models that can be used for decision-making and more effective management of dubas bug.

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