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1 **Modelling temperature-dependent bionomics of *Bemisia tabaci* (Q-**
2 **biotype)**

3

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8

9 **Abstract**

10 The influence of temperature (17, 21, 25, 30 and 35°C) on life history traits of a Q-
11 biotype *Bemisia tabaci* population on tomato is studied. Temperature dependent
12 relationships are characterized for immature developmental rate, immature survival,
13 fecundity, longevity and intrinsic rate of increase. Development time vary from 20
14 days at 30°C to 56 days at 17°C and the lowest thermal threshold is estimated at
15 10.2°C. The optimal temperature for immature development is 32.5°C. Total
16 fecundity (eggs per female) ranges from 105.3 (at 21°C) to 41 (at 35°C). The
17 longevity decreases with temperature increase. The intrinsic rate of increase ranges
18 from 0.0450 (at 17°C) to 0.123 (at 30°C). The functional relationships between
19 temperature and life-history parameters are used to evaluate the effect of temperature
20 on the population dynamics. Such mathematical relationships could provide a basis
21 for future development of population models.

22

23 **Key words**

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24 Temperature, bionomics, *Bemisia tabaci*, Q biotype, modelling

25

26 **Introduction**

27

28 The sweetpotato whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) is
29 one of the most serious agricultural pest on tomato *Lycopersicon esculentum* (Mill)
30 and other horticultural crops in tropical and subtropical temperature regions world-
31 wide. Damage may be caused directly by feeding on phloem or deposition of
32 honeydew, or indirectly by transmitting different types of plant viruses, such as the
33 tomato yellow leaf curl virus (Oliveira *et al.*, 2001), to a wide range of vegetable
34 crops. The potential of *B. tabaci* to develop resistance in response to intensive use of
35 pesticides has led to studies on integrated pest management strategies in which
36 biological control plays a central role, and significant advances have been made in
37 developing and implementing management systems (Gerling & Mayer, 1996;
38 Naranjo, 2001). As a general rule, any pest management programme should be based
39 on adequate knowledge of the main factors responsible for changes in population
40 dynamics. Life history parameters estimated under different biotic or abiotic
41 conditions provide the basic tools for among others, understanding changes in the
42 status of pest species (Poole, 1974; Dempster, 1975; Krebs, 1978; Southwood, 1978).
43 Because *B. tabaci* is a poikilothermic organism i.e. temperature influences the life
44 table components, it is important to take this factor into consideration in explaining
45 population ecology. A review by Drost *et al.* (1998) reported that biological
46 parameters of *B. tabaci* have been characterized for different temperatures, host
47 plants and biotypes. Among this vast amount of literature, the most complete work is
48 probably that of Wang & Tsai (1996) concerning B-biotype reared on aubergine.

49 The Q-biotype of *B. tabaci* was first characterized in samples collected in the south
50 of Spain and Portugal (Guiro *et al.*, 1997). Successive surveys showed that this
51 biotype is also present in Tunisia (Chermitti *et al.*, 1997), Morocco (Monci *et al.*,
52 2000), Egypt (De Barro *et al.*, 2000), Israel (Horowitz *et al.* 2003) and southern Italy
53 (Demichelis *et al.*, 2000; Simón *et al.*, 2003). Because of its high degree of
54 polyphagy and its ability to transmit a relatively wide range of plant viruses, the Q-
55 biotype is considered as a particularly dangerous biotype (Muñiz, 2000; Navas-
56 Castillo *et al.*, 2000). In spite of the wide distribution of the Q-biotype in the
57 Mediterranean basin, no complete published work is available currently on its life-
58 history parameters in relation to temperature when reared on tomato. The aim of the
59 present study was to characterize and analyze functional relationships between
60 temperature and life-history parameters and to evaluate the effect of temperature on
61 the dynamics of Q-biotype populations.

62

63 **Materials and methods**

64

65 *Whitefly source and host plant production*

66

67 In 2002, founders of *Bemisia tabaci* of the Q biotype were collected from a
68 greenhouse of tomato crop located in Alenya in the South of France (42°38'N;
69 2°58'E). The stock colony was reared and maintained on tomato plants of the cv
70 Hilario® (Royal Sluis, Enkhuizen, The Netherlands) in plastic cages placed in
71 climatic chambers at $25 \pm 1^\circ\text{C}$, and $60 \pm 5\%$ RH. Experiments were carried out using
72 progeny after more than 3 generations on Hilario.

73

74 *Development of immatures*

75

76 Young adults of *B. tabaci* (150 pairs: male and female) were placed in cubic
77 screened cages (50 x 50 x 50cm) each containing a young potted tomato plant. The
78 cages containing adults were maintained in a growth chamber at $25 \pm 1^\circ\text{C}$, $60 \pm 5\%$
79 RH in a LD 14:10 h photocycle. Whitefly adults were given 3 h to lay eggs. The
80 adults were then removed, leaves were observed under a stereo-microscope at 36X
81 magnification. Two eggs on the abaxial surface of 5 leaves were kept and excess
82 eggs were killed using an insect pin. Plants were then placed in growth chambers set
83 at 5 constant temperatures: 17, 21, 25, 30 and 35°C with six replicates. Once the eggs
84 hatched and the crawlers fixed on the leaf, young nymphs were identified
85 individually. Each nymph was observed daily until adult emergence, and the
86 transition from one stage to another was noted. Differences between developmental
87 times were tested by one-way ANOVA and means were separated by Newman–
88 Keuls test ($\alpha=0.05$). Statistical analyses were performed using XIStat 7.1
89 (Addinsoft). The influence of temperature (T) on developmental rate was described
90 by the model proposed by Logan *et al.* (1976):

91
$$DR = p1 \times \left[\exp (p2 \times (T - Ti)) - \exp \left(p2 \times (Tm - Ti) - \left(\frac{1}{p3} \right) \times (Tm - T) \right) \right]$$

92 where DR is the development rate which is the reciprocal of development time, Ti is
93 the lower temperature tested and Tm is the upper threshold derived from the
94 observations. The parameters, $p1$, $p2$ and $p3$ were estimated by regression. The
95 lowest thermal threshold for development (LTT) was calculated by the ratio: $LTT =$
96 a/b , a and b were determined by linear regression of the equation $DR = a + bT$, for
97 temperature (T) interval over which the relation was linear.

98 Differences between survival rates were tested using χ^2 test ($\alpha=0.05$). The
 99 relationship between temperature (T) and immature survival rate was described by
 100 the Curry & Feldman (1987) model:

101

$$SI = \frac{\left((T + 273) \times \exp \left(p1 - \left(\frac{p2}{(T + 273)} \right) \right) \right)}{\left(1 + \exp \left(p3 + \left(\frac{p4}{(T + 273)} \right) \right) \right) + \exp \left(p5 - \left(\frac{p6}{(T + 273)} \right) \right) \right)}$$

105

106 Where SI is survival of immatures, T is temperature in °C, and $p1$ to $p6$ are
 107 regression coefficients.

108

109 *Reproductive capacity and female longevity*

110

111 One newly emerged (<24 h) female and two males were placed in a clip-cage on the
 112 abaxial surface of new leaflets. For each temperature tested, 30 clip-cages were kept
 113 in growth chambers ($60 \pm 1\%$ RH, LD 14:10h photocycle). The clip-cages with
 114 insects were moved to new leaves daily and the number of eggs laid per female was
 115 counted until death of the female. Differences in fecundity and female longevity
 116 were compared with ANOVA followed by a Newman–Keuls tests ($\alpha=0.05$).
 117 Exponential functions were used to describe the influence of temperature on total
 118 fecundity and longevity.

119 Fecundity:

$$EN = p1 \times \left[(T^{p2}) \times \exp (p3 \times T) \right]$$

121

122 Where EN is total number of eggs laid per female; T is temperature in °C; and $p1$,
123 $p2$, $p3$ are regression coefficients.

124

125 Longevity:

$$126 \quad L = \exp [p1 + p2 \times T]$$

127

128 Where L is longevity per female in days; T is temperature in °C; and $p1$, $p2$: are
129 regression coefficients.

130

131 *Demographic parameters*

132

133 The net reproductive rate (R_0), the mean generation time (G), the intrinsic rate of
134 natural increase (r_m) and the finite rate of increase (λ) were determined using the
135 program developed by Hulting *et al.* (1990) in which the parameters are calculated
136 using the method recommended by Birch (1948). The program, based on Jackknife's
137 procedures, gives a variance and hence a standard error to each parameter calculated
138 enabling statistical comparison of values (Meyer, 1986). The relationship between r_m
139 and temperature was also described using the Logan *et al.* (1976) model (see above).

140

141 **Results**

142

143 *Development of immatures*

144

145 *B. tabaci* required 56 days at 17°C to complete its development from egg to adult,
146 but only 20 days at 35°C (Table 1). Between 17 and 30°C, the developmental time
147 was negatively correlated with temperature, but no significant difference was found
148 between 30 and 35°C ($P>0.05$). Values of Logan equation parameters were $p1 =$
149 0.0115 , $p2 = 0.0921$, $p3 = 0.3133$ ($R^2= 0.92$, $P<0.01$). Between 17 and 30°C, the
150 relation was linear and the *LTT* was estimated at 10.2°C (Fig. 1). The optimal
151 temperature for development, calculated from the derivative Logan equation, was
152 32.5°C.

153 Survival rates at 21, 25 and 30°C (Table 2) were not significantly different
154 ($\chi_w^2=0.695$, $P=0.707$) even if the highest percentage was measured at 25°C.
155 Temperature of 17°C had the greatest effect on immature development especially in
156 the 4th stadium. The curve obtained by fitting the Curry & Feldman model to the data
157 ($p1= -6.55$, $p2= -200.18$, $p3= -2986.08$, $p4= 865870$, $p5= 1353.19$, $p6= 6417118$,
158 $R^2=0.99$, $P <0.01$) described the influence of temperature very well and indicated that
159 17 and 35°C were close to the lower and upper thermal limits, respectively (Fig. 2).

160

161 *Longevity and reproductive capacity of females*

162

163 Temperature had a significant effect on the fecundity and longevity of females.
164 Longevity was negatively correlated with temperature. The longest life was recorded
165 at 17°C and the shortest at 35°C (Table 3). The pre-oviposition period was very short
166 (less than 24h) for almost all females tested and oviposition period was close to
167 longevity for the 5 temperatures tested. The relation between temperature and female
168 longevity (Fig. 3) was very well described by the exponential function ($p1= 5.02$,
169 $p2=-0.079$, $R^2=0.99$, $P <0.01$).

170 Except for 17°C, fecundity followed the same trend as longevity, i. e., was negatively
171 correlated with temperature. Figure 4 shows the influence of temperature on
172 fecundity ($p1= 9.9e-11$, $p2=12.8$, $p3=0.54$, $R^2=0.89$, $P<0.01$). Our results showed
173 that optimal fecundity was obtained from temperatures ranging between 21 and
174 25°C. The sex-ratio calculated for each treatment was not significantly different than
175 50% ($P>0.05$).

176

177 *Demographic parameters*

178

179 Parameters were calculated with the sex-ratio of *B. tabaci* set to 0.5. At the five
180 temperatures tested, the highest rate of increase (r_m) was obtained at 30°C and the
181 lowest at 17°C (Table 4). At 25, 30 and 35°C, the rates of increase were not
182 significantly different ($P>0.05$). The net reproductive rate was lower at 17°C and
183 35°C indicating the proximity of lower and upper thermal thresholds, respectively.
184 The curve (Fig.5) obtained by fitting the Logan model ($p1 = 0.019$, $p2 = 0.099$, $p3 =$
185 0.331 , $R^2= 0.99$, $P<0.01$) describes the influence of temperature on the rate of
186 natural increase very well. The optimal temperature for population development,
187 calculated from the derivative Logan equation was 31.3°C.

188 **Discussion**

189 Based on biological and ecological information published in the two last decades, the
190 immature developmental time of *B. tabaci* (from egg to adult) depends on the host
191 plant (Coudriet *et al.* 1985; Van Lenteren & Noldus, 1990; Bethke *et al.*, 1991;
192 Zalom *et al.*, 1995; Tsai & Wang, 1996; Muñiz & Nombela, 1997; Nava-Camberos
193 *et al.*, 2001) as well as on the whitefly populations or biotypes (Drost *et al.*, 1998;
194 Muñiz, 2000; Muñiz & Nombela, 2001). The developmental time of *B. tabaci*

195 recorded at 25°C ranges from 17.3 to 22.8 days when reared on either aubergine,
196 tomato, sweet potato, cucumber, bean or pepper. The present results show that on
197 tomato, the population of Q-biotype *B. tabaci* newly introduced in southern France
198 require 25.6 days to complete development from egg to adult at 25°C. In contrast,
199 Tsai & Wang (1996) report a shorter developmental time (17.96 days) for a Floridian
200 *B. argentifolii* population on tomato (cultivar Suny Hybrid) at 25°C. Based on the
201 model of Logan *et al.* (1976), the optimal temperature for the development of
202 immatures (32.5°C) is higher than that calculated for Florida, Mississippi, and Arizona
203 populations of *B. argentifolii* (29.9, 28.2, and 30.0°C, respectively) on aubergine
204 (Wang & Tsai, 1996). The optimum for *B. tabaci* biotypes on all host plants tested
205 ranges from 30 to 33°C (Drost *et al.*, 1998). The developmental threshold for
206 immatures belonging to the population studied here, estimated at 10.2°C, is lower
207 than that reported in the literature, which ranges from 10.8°C (Von Arx *et al.*, 1983)
208 to 12.5°C (Wang & Tsai, 1996).

209 Based on the range of temperatures tested here, survival rates of immature stages of
210 *B. tabaci* from egg to adult are higher on the tomato cultivar Hilario than those
211 reported on other cultivars of tomato (Tsai & Wang, 1996), Poinsettia (Enkegaard,
212 1993) and cotton (Wagner, 1995). Different responses to extreme temperatures, i.e.
213 in mortality of immatures, suggest that the Q-biotype population on tomato is more
214 tolerant to high temperatures (>33°C) than diverse *B. tabaci* populations on
215 aubergine (Wang & Tsai, 1996), cotton, and Poinsettia (Drost *et al.*, 1998).

216 Fecundity of *B. tabaci* is generally highly variable and depends on temperature
217 (Enkegaard, 1993), host-plant species (Liu & Oetting, 1994), and cultivar (Navon *et*
218 *al.*, 1991). Thus, the total number of eggs laid at 25°C by a Q-biotype female reared
219 on tomato *cv Hilario* (94.2 eggs) is considerably lower than that reported in the

220 literature for females reared on aubergine (223.67) (Wang & Tsai, 1996) and tomato
221 cv Suny Hybrid (165.55) (Tsai & Wang, 1996).
222 Wang & Tsai (1996) underline the importance of life table parameters to compare *B.*
223 *tabaci* populations and biotypes. On aubergine these authors (Wang & Tsai, 1996)
224 find a high intrinsic rate of increase at 25°C (0.192), 27°C (0.191), and 30°C (0.169)
225 compared with that found with the Q-biotype population on tomato at 25°C (0.106)
226 and 30°C (0.123). However, at 35°C, the net rate of increase of the B-biotype (0.073)
227 is lower than that of the French Q-biotype population (0.104). The tolerance to
228 extreme thermal conditions of the population newly introduced in France is also
229 confirmed by its shortest mean generation time recorded at 35°C (24.6 days).
230 The comparison between the results of this work and those from other studies (Wang
231 & Tsai, 1996; Muñiz & Nombela, 1996, 2001; Drost *et al.*, 1998; Nombela *et al.*,
232 2000, Muñiz, 2000) demonstrates clearly that the relationship between life-history
233 parameters and temperature is influenced highly by both insect biotype and host
234 plant species and variety. In spite of this high degree of variability within the *Bemisia*
235 complex, it is essential to better understand the population dynamics of the newly
236 introduced pest population in relation to temperature to improve control strategies
237 and evaluate its geographical extension capacity.

238

239 **References**

240

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- 348

Table 1. Developmental period (day \pm SE) of immature stages of *Bemisia tabaci* (Q biotype) at 5 constant temperatures.

Temp. (°C)	Stages						From egg to adult
	<i>n</i>	eggs	instar 1	instar 2	instar 3	instar 4	
17	80	21.5 \pm 0.09a	9.4 \pm 0.35a	7.5 \pm 0.93a	8.0 \pm 0.42a	9.4 \pm 0.33a	55.8 \pm 0.47a
21	80	14.0 \pm 0.09b	7.1 \pm 0.21b	4.1 \pm 0.18b	8.8 \pm 0.23a	5.6 \pm 0.18b	39.6 \pm 0.69b
25	80	10.4 \pm 0.13c	4.3 \pm 0.19c	3.7 \pm 0.16bc	3.8 \pm 0.15b	3.4 \pm 0.12c	25.6 \pm 0.26c
30	80	7.7 \pm 0.06d	3.2 \pm 0.13d	3.3 \pm 0.15c	3.5 \pm 0.15b	2.5 \pm 0.09d	20.2 \pm 0.24d
35	38	6.5 \pm 0.10e	3.9 \pm 0.17cd	3.3 \pm 0.21c	3.5 \pm 0.29b	3.3 \pm 0.22c	20.5 \pm 0.33d

Within columns means followed by the same letters are not significantly different ($P>0.05$).

Table 2. Survivorship (percentage) of immature stages of *Bemisia tabaci* (Q biotype) at 5 constant temperatures.

Temp. (°C)	Stages							
	<i>n</i> eggs	egg	instar 1	instar 2	instar 3	instar 4	<i>n</i> adults	From egg to adult
17	80	91.3	84.9	96.8	73.3	63.6	38	48c
21	80	98.7	98.7	93.4	93.0	97.0	64	83a
25	80	100	93.8	94.7	98.6	97.1	68	85a
30	80	100	95.0	96.1	93.2	97.1	66	82a
35	38	100	97.4	89.2	78.8	92.3	24	63b

Within columns means followed by the same letters are not significantly different ($P>0.05$).

Table 3. Fecundity (number of eggs per female \pm SE) and longevity (days \pm SE) of *Bemisia tabaci* (Q biotype) at 5 constant temperatures.

Temp. (°C)	<i>n</i>	Total fecundity	Longevity
17	30	49.3 \pm 6.7b	39.6 \pm 3.6a
21	30	105.3 \pm 10.4a	27.3 \pm 0.8b
25	30	94.2 \pm 12.3a	21.9 \pm 1.7c
30	30	58.6 \pm 10.4b	14.6 \pm 1.1d
35	30	41.0 \pm 5.6b	8.5 \pm 0.7e

Within columns means followed by the same letters are not significantly different ($P > 0.05$).

Table 4. Comparison of life table parameters of *Bemisia tabaci* (Q biotype) at 5 constant temperatures. n = number of females. r_m = Jackknife estimate of the intrinsic rate of increase. CI= confidence interval estimate of r_m . R_o = net reproductive rate (Standard error). G= mean generation time in day. λ = finite rate of increase = $\exp(r_m)$.

Temp. (°C)	Parameters					
	<i>n</i>	r_m	95%CI	R_o	G	λ
17	30	0.045c	0.044-0.046	29.8 (0.2)	77.2	1.05
21	24	0.079b	0.078-0.080	52.5 (0.1)	49.9	1.08
25	18	0.106a	0.090-0.121	39.5 (5.5)	35.1	1.11
30	24	0.123a	0.103-0.142	23.6 (4.3)	26.5	1.13
35	23	0.104a	0.087-0.119	12.3 (1.8)	24.6	1.11

Within columns means followed by the same letters are not significantly different (P>0.05).

Figure captions

Fig. 1. Influence of temperature on development time of *Bemisia tabaci* (Q biotype). Points: experimental values. curve simulated by Logan *et al.* (1976).

Fig. 2. Influence of temperature on survivorship of *Bemisia tabaci* (Q biotype). Points: experimental values. curve simulated by Curry & Feldman model (1987)

Fig. 3. Influence of temperature on female longevity of *Bemisia tabaci* (Q biotype). Points: experimental values. curve simulated by exponential model.

Fig. 4. Influence of temperature on fecundity of *Bemisia tabaci* (Q biotype). Points: experimental values. curve simulated by multiplicative exponential model.

Fig. 5. Influence of temperature on intrinsic rate of increase of *Bemisia tabaci* (Q biotype). Points: experimental values. curve: simulated by Logan *et al.* (1976) model.

Fig. 1.

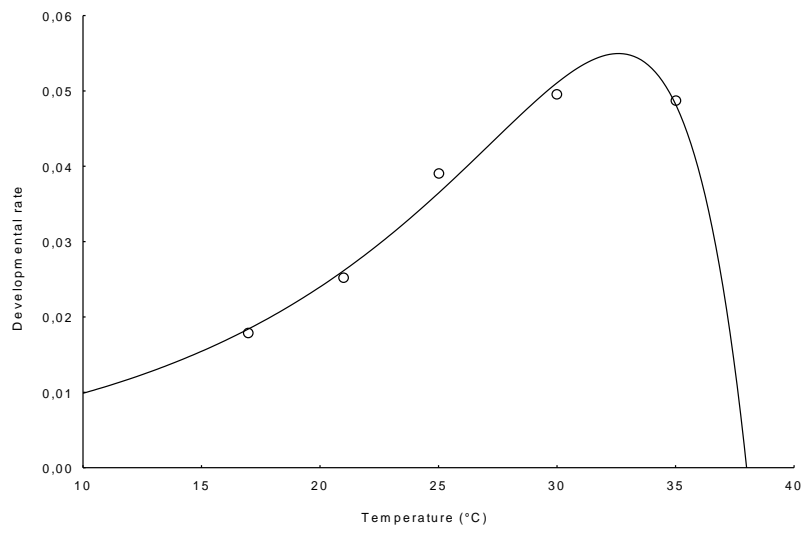


Fig. 2.

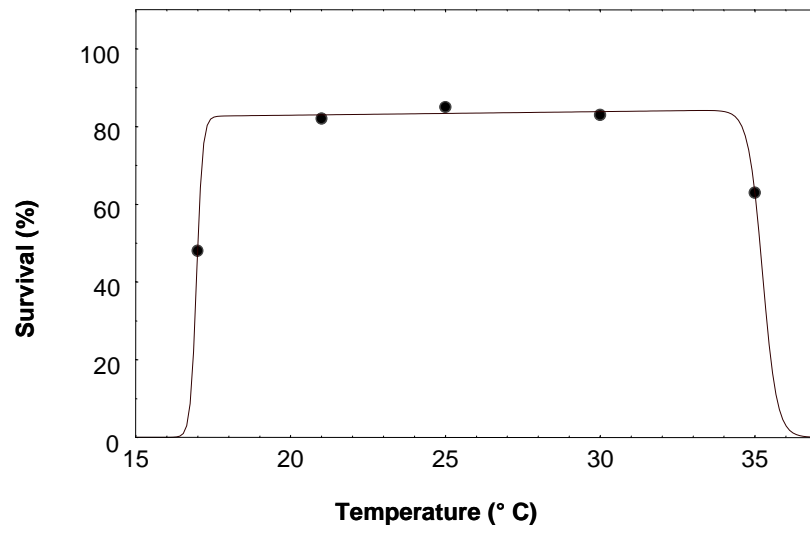


Fig. 3

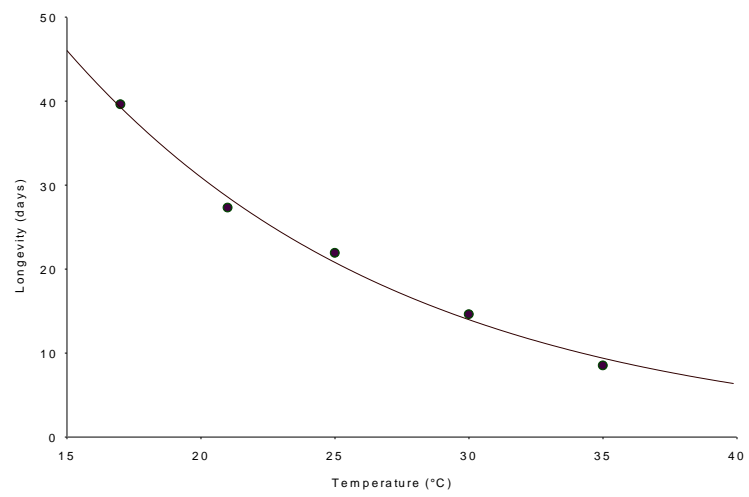


Fig. 4.

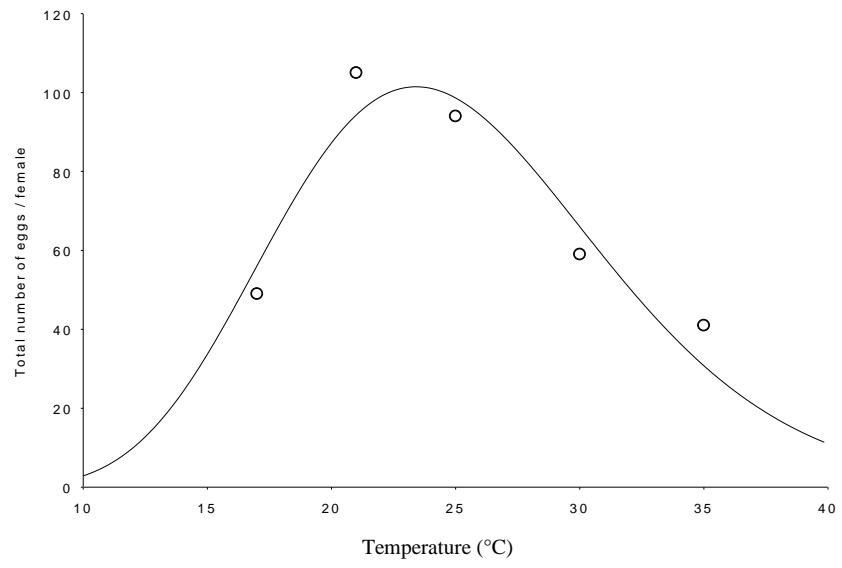


Fig. 5.

