Life History of the Mealybug, *Maconellicoccus hirsutus* (Hemiptera: Pseudococcidae), at Constant Temperatures

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ABSTRACT Important life history parameters of the mealybug, *Maconellicoccus hirsutus* (Green), were characterized on hibiscus (*Hibiscus rosa-sinensis* L.) cuttings at six constant temperatures between 15 and 35°C. The development of *M. hirsutus* was the fastest at 27°C, where the mealybugs completed development in ≈29 d. The lower (T_{min}) and upper (T_{max}) developmental thresholds and the optimal developmental temperature (T_{opt}) for the development of female mealybugs were estimated as 14.5, 35, and 29°C, respectively. The thermal constant (K), which is the number of temperature-day or degree-day units required for development, of the females was 347 DD. The original distribution range prediction (based on T_{min} = 17.5°C and K = 300 DD) indicated that *M. hirsutus* could complete at least one generation in all of the continental United States. However, results of this study suggested that the distribution range of *M. hirsutus* may expand northward because of the lower T_{min}, and the predicted number of generations in a year may be lower because of the higher K required to complete each generation. The average cumulative survival rate of *M. hirsutus* at 25 and 27°C was 72%, which was significantly higher than 51 and 62% at 20 and 30°C, respectively. *M. hirsutus* reproduced sexually, with each mated female producing 260–300 eggs between 20 and 27°C but only ≈100 eggs at 30°C. Female longevity was reduced from 28 d at 20°C to 19–21 d at 25–30°C. At 27°C, the net reproductive rate (R_o) was estimated at 165 ♀/♀, the intrinsic rate of population increase (r_m) was 0.119 (♀/♀/d), the generation time (T_G) was 43 d, and the doubling time (DT) was 5.8 d. The life table statistics suggested that the currently released biological control agents, which have higher r_m than *M. hirsutus*, will be able to complete more generations than the mealybug within the tested temperature range; thus, they are effective against *M. hirsutus*.

KEY WORDS life table analysis, developmental thresholds, survivorship, reproduction, distribution

Maconellicoccus hirsutus (Green) (Hemiptera: Pseudococcidae) is a serious pest of many horticultural and agronomic crops in the world, causing severe distortion of leaves and new shoots and the eventual death of host plants (Kairo et al. 2000). *M. hirsutus* was widespread in the tropical and subtropical regions of Asia, Africa, and Australia before its accidental introduction into the Caribbean and the Americas (Williams 1996). *M. hirsutus* was detected in Grenada in 1994, after which it rapidly spread to most of the Caribbean and parts of Belize and Venezuela (Kairo et al. 2000). The first reported establishment of *M. hirsutus* in the United States was in Hawaii in 1983 (Beardsley 1985), followed by California in 1999 (Roltsch et al. 2006), Florida in 2002 (Hoy et al. 2002), and Louisiana in 2006 (LDAF 2006). The introduction of two exotic parasitoids, *Anagyrus kamali* Moursi and *Gyranusoidea indica* Shafee et al. (both Hymenoptera: Encyrtidae), in combination with the already established ladybeetle *Cryptolaemus montrouzieri* Mulsant (Coleoptera: Coccinellidae), seemed to successfully control the mealybug populations in California (Roltsch et al. 2006) and Florida (Amalin et al., unpublished data).

Despite successful biological control, the risk of spreading *M. hirsutus* through shipments of infested ornamentals remains high. Some of the crops that are expected to be most impacted include avocado, citrus, cotton, peanuts, nursery crops, soybean, and vegetables (Moffitt 1999). *M. hirsutus* was estimated to cause damage of more than $162 million in Florida and $675 million in the entire predicted distribution (Ranjan 2004). Scientists at the U.S. Department of Agriculture have predicted the distribution of *M. hirsutus* using different simulation models, such as CLIMEX and NAPPFAST (North Carolina State University–APHIS Plant Pest Forecast System). Based on the climatic data from infested areas in Asia, Africa, and Australia, the CLIMEX model predicted that *M. hirsutus* could spread to most southern states in the United States

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(USDA 1998). The NAPPFAST model predicted that *M. hirsutus* could complete at least one generation in all of the continental United States (Borchert et al. 2005). The predicted range was more restricted when local freezing conditions were incorporated (Borchert et al. 2005). The life history parameters used by NAPPFAST were estimated from data presented in a single study (Babu and Azam 1987). These distribution models could benefit from more comprehensive life history data.

Despite the economic importance of *M. hirsutus*, there is a lack of detailed life history data on the species. Mani (1989) provided a brief review of the biology, natural enemies, and host range of *M. hirsutus.* A female develops through three nymphal instars and a male through four instars before adulthood. The developmental period is dependent on temperature, ranging from 23 to 35 d. *M. hirsutus* feed on >125 plant species, causing malformation of shoots and leaves, providing the growth of sooty mold, and lowering crop yield. Sixteen parasitoid species and 30 predator species have been reported as natural enemies of *M. hirsutus.* Some of these natural enemies, such as *A. kamali*, *G. indica*, and *C. montrouzieiri*, have been used extensively and successfully to control *M. hirsutus.*

Many earlier reports on the life history of *M. hirsutus* were conducted at either a single constant temperature (Persad and Khan 2002, Serrano and Lapointe 2002) or fluctuating temperature regimens (Babu and Azam 1987). Researchers also used different host plants for the experiments because of the polyphagous nature of *M. hirsutus* and the crops of concern at the time (Mani 1989, Serrano and Lapointe 2002). These differences in methodologies complicated the effort in estimating important life history parameters of *M. hirsutus* and the use of these data in predicting the pest distribution.

We present a comprehensive study on the life history of *M. hirsutus* conducted on hibiscus (*Hibiscus rosa-sinensis* L.) at six constant temperatures (15–35°C). We determined the developmental thresholds, thermal constant, fecundity, survivorship, and important life table parameters of *M. hirsutus.* The ultimate goals of this study were to provide a better understanding of the life history of *M. hirsutus*, to verify important life history parameters, and to provide such information for an improved prediction of the pest's distribution in the United States.

Materials and Methods

Maintenance of Insect Colony and Host Plants. A colony of *M. hirsutus* was initiated in January 2005 with adult females collected from infested hibiscus plants in Miami, FL. The colony was maintained on sprouted potatoes (*Solanum tuberosum* L.) in an incubator (818 Illuminated Incubator; Precision, Chicago, IL) at 28 ± 3°C, 65 ± 5% RH, and complete darkness.

Hibiscus plants obtained from a local nursery were used as the host plants for *M. hirsutus* in this study. The plants were maintained outdoors under overhead irrigation for 1 mo before the commencement of the experiments. The mealybugs often feed on the young stems and petioles of hibiscus plants. Thus, hibiscus cuttings were prepared from young shoots with the leaf petioles and part of the stems (1.5–2.0 cm) directly above the petioles exposed for mealybug infestation. The stem below the petiole was inserted into a cup of water through a hole drilled on the bottom of a petri dish (20 by 100 mm). Each petri dish was covered with the lid and rested on top of a cup of water. Most hibiscus cuttings rooted within 3 wk.

Development and Survivorship. The influence of six constant temperatures (15, 20, 25, 27, 30, and 35 ± 1°C) on the developmental and survival rates of *M. hirsutus* was examined in the laboratory at the USDA–ARS Subtropical Horticulture Research Station, Miami, FL. The environmental chambers (TC1 model; Environmental Growth Chambers, Chagrin Falls, OH) were maintained at constant temperatures, 65 ± 2% RH, and 14:10 (L:D)-h photoperiod. The relative humidity was within the range of average monthly afternoon relative humidity recorded in Miami (54–67%; NCDC 2005).

Thirty gravid females were collected from the laboratory colony and incubated on hibiscus cuttings until oviposition at each temperature treatment. Ten eggs were collected from each ovipositing female within 24 h of deposition, transferred onto the petiole of a hibiscus cutting, and incubated in one of the six constant temperatures. To encourage settlement of the crawlers (i.e., first-instar nymphs), the environmental chambers were maintained at complete darkness for 72 h during the course of egg eclosion. Mealybugs on each cutting represented a cohort and a replicate. A total of 30 cohorts or replicates were prepared at each temperature treatment.

The mealybug cohorts were examined every 24 h, and the development and survival of each developmental stadium were recorded. Successful development from one instar to the next was indicated by the presence of exuviae. The exuviae of the third- and fourth-instar males was pushed to the end of the loosely woven tests (or puparia) and were clearly visible. Survival rate for each stadium was presented as the percentage of individuals that successfully developed to the next stadium. The sex of individual mealybugs could not be determined at egg and crawler stages. Thus, the cumulative survival rates from eggs to adults were determined by dividing the total numbers of adults by the numbers of eggs used to initiate the cohorts. Secondary sex ratio was presented as the proportion of adult females in the total adult population.

One-way analysis of variance (ANOVA) was used to determine the effect of temperature on the stage-specific and cumulative developmental times, survival rate, and sex ratio of *M. hirsutus* at a significant threshold of 0.05 (PROC GLM; SAS Institute 1999). The survival rate and sex ratio were arsine-transformed to standardize the variance before the statistical analysis. Tukey's honestly significant difference (HSD) test was used to separate the means.

Thermal Requirements. The lower developmental threshold (T_{min}) and the thermal constant (K) of *M. hirsutus* were estimated using the thermal summation model, which describes the relationship between the developmental rate of insects and the ambient temperature in a linear regression equation (Wagner et al. 1984, Trudgill et al. 2005):

$$1/D = bT + a,$$

where 1/D is the developmental rate (in day^{-1}), T is the ambient temperature (in °C), and a (in day^{-1}) and b (in $day^{-1} \cdot °C^{-1}$) are the estimated linear regression parameters (PROC REG; SAS Institute 1999). Because of a decline or cessation of development at high temperatures, only the developmental rates between 15 and 27°C were analyzed with the linear thermal summation model. The lower developmental threshold was calculated by $T_{min} = -a/b$. The thermal constant ($K = 1/b$) is the number of heat units or degree-days above T_{min} that was needed for the completion of a developmental stage.

The upper developmental threshold (T_{max}) and the optimal temperature for development (T_{opt}) were estimated with the nonlinear Logan 6 model (Logan et al. 1976). The Logan 6 model does not estimate a lower developmental threshold because the asymptote does not intercept with the temperature axis. Developmental rates of each developmental stage were fitted to the model

$$1/D = \psi\left[\exp(\rho T) - \exp\left(\rho T_{max} - \frac{T_{max} - T}{\Delta T}\right)\right],$$

and the parameters (ψ, ρ, T_{max}, and ΔT) were estimated using the nonlinear regression procedure (PROC NLIN; SAS Institute 1999). The parameter ψ is the developmental rate at the base temperature, ρ is the biochemical reaction rate as T increases to T_{opt}, and ΔT is the difference between T_{opt} and T_{max} when thermal breakdown becomes the overriding influence. The optimum temperature for development was calculated as

$$T_{opt} = T_{max}\left[1 + \varepsilon\left(\frac{\ln(\varepsilon b_o)}{1 - \varepsilon b_o}\right)\right],$$

where $\varepsilon = \Delta T/T_{max}$ and $b_o = \rho \times T_{max}$ (Logan et al. 1976).

Reproduction and Adult Longevity. The influence of four constant temperatures (20, 25, 27, and 30 ± 1°C) on the fecundity, reproductive period, and adult longevity of *M. hirsutus* was studied using adult mealybugs collected from the development and survivorship experiment. The adult mealybugs were collected within 24 h of eclosion, and the females were isolated individually on hibiscus cuttings. One or two adult male mealybugs were introduced into each petri dish 3 d after the female eclosion. The adult mealybugs were kept at the assigned temperatures until death. Adult longevity was recorded as the duration between adult eclosion and death. The ovisacs produced by individual female mealybugs were removed every 24 h, and the eggs were counted. The duration from adult eclosion to oviposition (i.e., prereproductive period) and the numbers of days that the females reproduced (i.e., reproductive period) were determined. The fecundity and longevity of a total of 30 females and varying numbers of males were determined at each constant temperature. Females that did not reproduce were excluded from the data analyses.

The possibility of parthenogenetic reproduction by *M. hirsutus* was also investigated in this study. Thirty adult females were isolated on individual hibiscus cuttings within 24 h of their eclosion at 25°C. No adult males were introduced into the petri dishes; thus, the females remained virgins. The females were examined every 24 h for reproduction.

The effect of temperature on fecundity, reproductive periods, and adult longevity was analyzed with ANOVA, followed by Tukey's HSD test to separate the means at $\alpha = 0.05$ (SAS Institute 1999).

Life Table Analysis. The effect of four constant temperatures (20, 25, 27, and 30 ± 1°C) on the population growth and age structure of *M. hirsutus* was assessed based on various life table parameters. Data on survivorship and reproduction were used to construct a life table of l_x (age-specific survival rate) and m_x (age-specific fecundity) with an age increment of 1 d. The age-specific fecundity was the average number of female eggs produced by each female at a specific age (x). In the reproduction experiment, eggs were not reared to adulthood; therefore, sex of the offspring could not be determined. Instead, m_x at a specific temperature was obtained by multiplying the average daily fecundity with the proportion of females that was calculated from the developmental experiment at that temperature. The formulae for estimating the life table parameters of female *M. hirsutus* at each temperature were (Carey 1993):

gross reproductive rate, $GRR = \sum m_x$;

net reproductive rate, $R_o = \sum(l_x m_x)$;

mean generation time, $T_G = \dfrac{\sum(x l_x m_x)}{\sum(l_x m_x)}$;

intrinsic rate of increase, $r_m = (\ln R_o)/T_G$;

finite rate of increase, $\lambda = \exp(r_m)$;

doubling time, $DT = \ln 2/r_m$; and stable age distribution (Birch 1948),

$$C_x = \frac{l_x \exp(-r_m x)}{\sum_{x=0}[l_x \exp(-r_m x)]}.$$

Results

Duration of Development and Thermal Requirements. Eggs of *M. hirsutus* held at 20°C hatched in 16 d, which was longer than those at 30 and 35°C (6 d; Table 1). No eggs eclosed at 15°C. Developmental rates increased as the temperature increased between 20 and 27°C for both male and female mealybugs. However, the nymphal development of females decreased at

Table 1. Mean number of days (±SEM) for each developmental stadium of *M. hirsutus* (Green) reared on hibiscus cuttings at four constant temperatures

Temp. (°C)	Developmental stadia								
	Egg	First	Second		Third		Fourth[a]	Cumulative	
			Female	Male	Female	Male	Male	Female	Male
20	16.3 ± 0.1a	24.4 ± 0.3a	13.4 ± 0.4a	10.0 ± 0.8a	12.3 ± 0.2a	3.7 ± 0.3a	12.3 ± 0.4a	66.4 ± 0.4a	66.7 ± 0.5a
25	9.3 ± 0.1b	9.4 ± 0.2b	7.2 ± 0.6b	5.7 ± 0.2b	6.4 ± 0.2c	3.6 ± 0.2a	4.2 ± 0.3b	31.3 ± 0.4b	32.4 ± 0.2b
27	8.6 ± 0.1c	8.1 ± 0.2c	5.6 ± 0.2c	6.7 ± 0.2b	6.9 ± 0.3c	1.7 ± 0.1b	4.6 ± 0.3b	29.2 ± 0.4c	29.8 ± 0.3c
30	6.7 ± 0.1d	7.7 ± 0.2c	8.3 ± 0.4b	6.9 ± 0.4b	10.6 ± 0.5b	1.9 ± 0.3b	4.7 ± 0.5b	33.3 ± 0.7b	27.5 ± 0.7c
35	6.3 ± 0.1e	—	—	—	—	—	—	—	—
ANOVA statistics									
n	154	120	119	96	119	93	91	112	91
F	2138.22	1460.75	69.94	14.49	76.43	22.87	113.14	1167.37	1364.26
df	4,150	3,117	3,116	3,93	3,116	3,90	3,88	3,109	3,88
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Means within a column followed by the same letters are not significantly different at $\alpha = 0.05$ (Tukey's HSD test).
[a] Only male nymphs achieved the fourth nymphal instar. Female mealybugs have only three nymphal instars.

30°C, where the developmental time of second- and third-instar females were between those at 20 and 25°C (Fig. 1). The cumulative developmental time for female *M. hirsutus* was reduced from 66 d at 20°C to 29 d at 27°C and was increased to 33 d at 30°C (Table 1). In contrast, the developmental rates of immature males were not reduced at 30°C and were similar to those at 25 and 27°C (Fig. 1). The cumulative developmental time of male mealybugs was the shortest at 30°C (27.5 d), which was similar to that at 27°C (29.8 d) but less than one half of that at 20°C (66.7 d; Table 1).

The linear thermal summation equations fit ($R^2 > 0.90$) the developmental rates of all life stages of *M. hirsutus* between 20 and 27°C (Table 2; Fig. 1). The estimated lower developmental thresholds (T_{min}) were 14.5, 15.2, and 15.0°C for egg, female nymphal, and male nymphal developments, respectively. The estimated T_{min} for the cumulative developments of females and males were 14.5 and 14.3°C, respectively. The estimated thermal constants were 101.7 DD for eggs, 230.9 DD for female nymphal development, and 245.1 DD for male nymphal development. A total of 347.2 DD was required for the complete development of females, and 363.6 DD was required for the males.

The nonlinear Logan 6 model also provided sufficient fit to the data (Table 2; Fig. 1). The upper developmental threshold (T_{max}) and the optimal developmental temperature (T_{opt}) of eggs were estimated at 39.8 and 33.4°C, respectively. The T_{max} for the nymphal and cumulative developments of males and females was estimated at 35°C. The T_{opt} for the nymphal and total developments of males (both 29.7°C) was slightly higher than that of the females (28.8 and 29.0°C, respectively).

Survivorship and Sex Ratio. The extreme high (35°C) and low (15°C) temperatures were detrimental to the survival of *M. hirsutus* (Table 3). No eggs showed signs of embryonic development (segmentation and development of eyes visible through the translucent chorion) after incubating for 60 d at 15°C. More than 87% of eggs hatched between 20 and 27°C compared with only 47% at 35°C. All of the fourth-instar immature males successfully emerged as adults at 20 and 25°C. Overall, 72% of the eggs incubated at 25 and 27°C completed development to adults, which was higher than 51 and 62% at 20 and 30°C, respectively.

The secondary sex ratio at 30°C was significantly higher than those at lower temperatures (ANOVA: $F = 3.11$; df = 3,116; $P = 0.0291$). Females made up 78 ± 4, 74 ± 4, 72 ± 4, and 85 ± 3% of the total adult populations at 20, 25, 27, and 30°C, respectively.

Adult Longevity and Reproduction. *Maconellicoccus hirsutus* reproduced sexually. Virgin females did not reproduce after 2 mo in isolation. Temperature significantly impacted adult longevity, reproductive periods, and fecundity of mated *M. hirsutus.* The pre-reproductive period was the longest at 20 (12.6 ± 0.9 d) and 30°C (12.6 ± 0.5 d) and the shortest at 27 (10.8 ± 0.9 d) and 25°C (9.3 ± 0.4 d) ($F = 5.03$; df = 3,85; $P = 0.0029$). The reproductive period of *M. hirsutus* was the longest at 20°C (11 d), whereas those at 25–30°C reproduced for 7–8 d ($F = 7.77$; df = 3,85; $P = 0.0001$). Female mealybugs incubated at 30°C produced a significantly lower number of eggs (103 ± 8 eggs per female; $F = 15.03$; df = 3,85; $P < 0.0001$). The fecundity of *M. hirsutus* was similar at 20 (260 ± 24 eggs), 25 (300 ± 32 eggs), and 27°C (274 ± 23 eggs).

Female longevity was the longest at 20°C where the female *M. hirsutus* survived for 28.2 ± 1.1 d after adult eclosion ($F = 15.23$; df = 3,85; $P < 0.0001$). The longevities of females were similar at 25 (21.2 ± 0.7 d), 27 (19.9 ± 0.9 d), and 30°C (19.5 ± 1.3 d). Adult male *M. hirsutus* were short-lived, and their longevity decreased as the temperature increased ($F = 23.37$; df = 3,125; $P < 0.0001$). Adult males lived for 3.4 ± 0.3 d at 20°C, followed by 2.5 ± 0.1 d at 25 and 27°C, and only 1.4 ± 0.1 d at 30°C.

Life History Parameters. The age-specific survivorship (l_x) and fecundity (m_x) are presented in Fig. 2. The gross and net reproductive rates (GRR and R_o, respectively) increased with temperature until the highest values were reached at 27°C and were reduced to their lowest values at 30°C (Table 4). The generation time (T_G) was increased from 41 d at 25°C to 82 d at 20°C. The intrinsic rate of increase (r_m) was lower

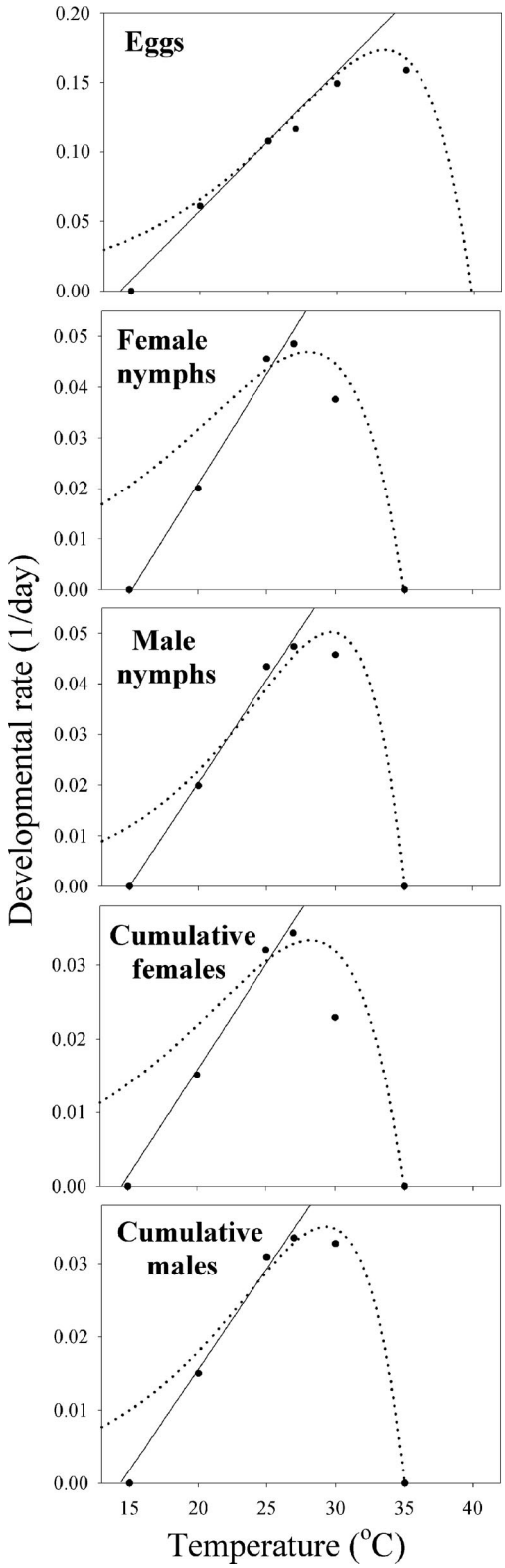

Fig. 1. Relationship between temperature and developmental rates of developmental stages of *M. hirsutus* (Green reared on hibiscus cuttings at four constant temperatures (15–27°C). The solid dots are the average developmental rates. The solid lines depict the results of the best-fitted linear thermal summation model. The dotted lines are the best-fitted nonlinear Logan 6 model.

at 20°C (0.06) than at 25 and 27°C (0.12 for both temperatures). The finite rate of increase (λ) followed the same trend as r_m, with the highest estimated value of 1.13 at 25 and 27°C. A population of *M. hirsutus* required only ≈6 d to double its number at 25 and 27°C, but the doubling time (DT) was increased to 8 and 13 d at 30 and 20°C, respectively.

The stable age distributions of females in various developmental stadia were different among the constant temperatures (Table 4). When a *M. hirsutus* population reared at 25°C achieved stable age distribution, i.e., when the population grew at a constant rate, the population was composed of 67% eggs, 25% crawlers, 5% second-instar nymphs, 2% third-instar nymphs, 1% prereproductive adults, and 0.5% reproductive adults. Eggs also made up the largest proportion of the mealybug population that achieved stable age distribution at 20°C. The lowest contribution of eggs and the highest contribution of adult females were found at 27 and 30°C.

Discussion

Increased temperature accelerated the development of female *M. hirsutus* from an estimated lower developmental threshold of 14.5°C up to a maximum rate at 29°C, after which the development decelerated until it was predicted to finally cease at 35°C. The developmental time of females was >2 mo at 20°C but was halved at 27°C. The duration of development between 20 and 27°C reported here is similar to other studies. Serrano and Lapointe (2002) reported a cumulative duration of 29.6 d when females were reared on Japanese pumpkin (*Cucurbita moschata* Duchesne) at 27 ± 2°C, 70% RH, and complete darkness. Development of female mealybugs on whole hibiscus plants was completed in ≈28 d at 27°C, 58% RH, and 12-h photoperiod (Persad and Khan 2002). When reared on pumpkin fruits at fluctuating temperatures in the field cages, *M. hirsutus* completed development in 48 d at a mean temperature of 25°C, 29 d at 27.2°C, and 25.5 d at 29.5°C (Babu and Azam 1987).

The lower developmental thresholds (T_{min}) and thermal constants (K) estimated from Babu and Azam (1987) were 19.4°C and 60.8 DD for egg eclosion and 17.5°C and 300 DD for complete adult development, respectively (J.H.C., unpublished data). In this study, when *M. hirsutus* was reared on hibiscus cuttings, the estimated T_{min} was lower (14.5°C for both eggs and complete female development) and K was higher (101.7 DD for eggs and 347.2 DD for females) than those estimated from data in Babu and Azam (1987). Seasonality might have influenced the development of the mealybugs in Babu and Azam (1987), thus resulting in different reported developmental durations

Table 2. Summary of statistics and the estimates (±SE) of the fitted parameters of linear thermal summation model and nonlinear Logan 6 model

Statistics parameters	Developmental stadia				
	Egg	♀ nymphal	♂ nymphal	Total ♀	Total ♂
Thermal summation model: $1/D = a + bT$					
F	5289.3	797.84	1011.85	1196.17	1436.88
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
R^2	0.9782	0.9007	0.9354	0.9315	0.9535
a ± SE	−0.142 ± 0.003	−0.066 ± 0.004	−0.061 ± 0.003	−0.042 ± 0.002	−0.039 ± 0.002
b ± SE	0.010 ± 0.001	0.004 ± 0.001	0.004 ± 0.001	0.003 ± 0.001	0.003 ± 0.001
Logan 6 model: $1/D = \psi \times \left[\exp(\rho T) - \exp\left(\rho T_{max} - \frac{T_{max} - T}{\Delta T}\right)\right]$					
F	10298.2	1506.4	3030.11	3346.51	4804.19
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
SS_R	0.0119	0.00624	0.00218	0.00112	0.00096
SS_{CT}	0.1970	0.0559	0.0543	0.0255	0.0305
Pseudo-R^2	0.9396	0.8884	0.9599	0.9561	0.968
ψ ± SE	0.134 ± 0.938	0.104 ± 1.420	0.050 ± 0.500	0.061 ± 0.568	0.036 ± 0.280
ρ ± SE	0.156 ± 0.008	0.160 ± 0.010	0.188 ± 0.008	0.167 ± 0.007	0.189 ± 0.006
T_{max} ± SE	39.8 ± 0.3	35.0 ± 0.1	35.0 ± 0.1	35.0 ± 0.1	35.0 ± 0.1
ΔT ± SE	6.365 ± 0.087	6.208 ± 0.099	5.299 ± 0.075	5.974 ± 0.098	5.262 ± 0.079

SS_R, residual sums of squares; SS_{CT}, corrected total sums of squares; pseudo-R^2, $1 - SS_R/SS_{CT}$.

from this study. The differences in the female developmental time reared on five host plant species and a meridic diet also indicated the influence of host plant species (Serrano and Lapointe 2002).

The estimated T_{min} of *M. hirsutus* was higher and K was lower than those of many mealybug species. Arai (1996) reported that the respective T_{min} and K of nymphal development were 11.7°C and 338 DD for *Pseudococcus citriculus* Green, 7.7°C and 401 DD for *P. citri*, and 8°C and 519 DD for *Planococcus kraunhiae* (Kuwane), respectively. The estimated T_{min} of *Placnoccus citri* (Risso) was 10.90C, and the K of females ranged between 289 to 365 DD (Laflin and Parella 2004). Using data presented in Chong et al. (2003), the T_{min} was estimated at 7.4°C and K at 540.5 DD for complete development of female Madeira mealybug, *Phenacoccus madeirensis* Green. However, the T_{min} and K of the pink sugarcane mealybug, *Saccharicoccus sacchari* (Cockerell), were 17.0°C and 339.6 DD, respectively (Rae and De'ath 1991). The T_{min} and T_{max} of *Planococcus ficus* (Signoret) were estimated at 16.6 and 35.6°C, respectively (Walton and Pringle 2005).

Based on T_{min} of 17.5°C and K of 300 DD estimated from data presented in Babu and Azam (1987), the NAPPFAST model predicted that *M. hirsutus* could complete at least one generation in all of the continental United States (Borchert et al. 2005). The distribution range prediction by the NAPPFAST model can be improved with the results of this study, which is more comprehensive than Babu and Azam (1987). The T_{min} estimated in this study suggested that *M. hirsutus* was capable of surviving at an ambient temperature >15°C. Thus, we expect the predicted distribution of *M. hirsutus* to expand to more northern latitude than that originally predicted by Borchert et al. (2005) and to include regions with a lower ambient temperature (e.g., southern Canada). A higher K estimated in this study suggested that *M. hirsutus* required a higher number of degree-days to complete development than that estimated from Babu and Azam

Table 3. Mean (±SEM) survival rate (in %) for each developmental stadium of *M. hirsutus* (Green) reared on hibiscus cuttings at six constant temperatures

Temperature (°C)	Egg	First	Second	Third		Fourth[a]	Cumulative
				Female	Male	Male	
15	0c	—	—	—	—	—	0c
20	91 ± 1a	58 ± 4b	100	99 ± 9b	88 ± 3b	100a	51 ± 2b
25	89 ± 2a	86 ± 3a	94 ± 2	97 ± 1a	92 ± 7ab	100a	72 ± 3a
27	87 ± 4a	87 ± 4a	73 ± 5	96 ± 2a	100a	95 ± 6b	72 ± 3a
30	91.2 ± 2a	81 ± 3a	88 ± 4	94 ± 2a	96 ± 4ab	87 ± 7b	62 ± 4a
35	46.7 ± 8b	0c	—	—	—	—	0c
ANOVA statistics							
n	198	168	119	119	96	92	180
F	59.74	89.63	1.27	7.47	4.04	3.05	71.33
df	5,193	4,164	3,116	3,116	3,93	3,89	5,175
P	<0.0001	<0.0001	0.2875	0.0001	0.0095	0.0327	<0.0001

Means within a column followed by the same letters are not significantly different at $\alpha = 0.05$ (Tukey's HSD test).
[a] Only male nymphs achieved the fourth nymphal instar. Female mealybugs have only three nymphal instars.

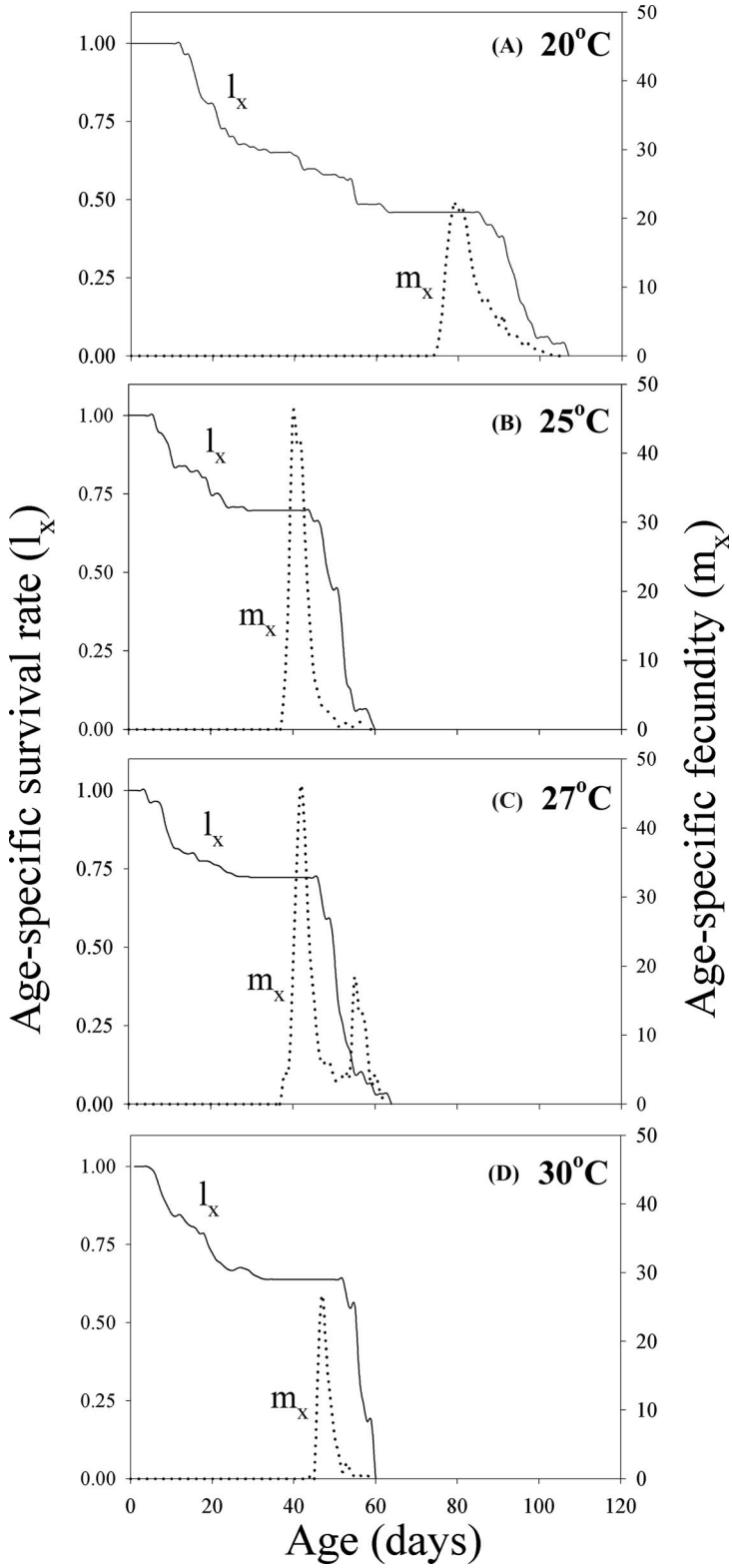

Fig. 2. Age-specific survival rate (l_x) and age-specific fecundity (m_x) of *M. hirsutus* (Green) reared on hibiscus cuttings at four constant temperatures (20–30°C).

Table 4. Life history parameters of *M. hirsutus* (Green) reared on hibiscus cuttings at four constant temperatures

Life history parameters	Temperatures (°C)			
	20	25	27	30
Gross reproductive rate, GRR (♀/♀)	217.9	229.8	301.2	88.8
Net reproductive rate, R_o (♀/♀)	93.4	155.6	165.8	56.0
Generation time, T_G (d)	81.8	41.2	43.0	47.5
Intrinsic rate of increase, r_m (♀/♀/d)	0.056	0.112	0.119	0.085
Finite rate of increase, λ (♀/♀/d)	1.057	1.130	1.126	1.088
Doubling time, DT (d)	12.5	5.7	5.8	8.2
Stage age distribution for females (%)				
Eggs	65.6	66.9	34.9	35.5
First instar	27.9	24.5	32.6	25.4
Second instar	3.9	4.7	9.6	18.5
Third instar	1.5	2.1	9.2	10.6
Pre-reproductive adult	0.8	1.3	8.7	7.0
Reproductive adult	0.3	0.5	5.0	3.0

(1987). Therefore, we expect the number of viable generations of *M. hirsutus* in a year to be lower than originally predicted by Borchert et al. (2005). Other environmental factors, such as photoperiodism, dormancy, diapause, and cold tolerance, will determine the eventual distribution of this species. When the assumption of no permanent establishment in regions with a total of 75 d below 0°C was imposed to their prediction, Borchert et al. (2005) showed that the predicted distribution range of *M. hirsutus* was reduced to the Pacific coast, southwestern, and southern states. Future regulatory and management efforts against *M. hirsutus* should take into consideration the anticipated northward expansion in distribution and reduction in the number of viable generations.

In addition to the predictive models, the distribution range of *M. hirsutus* could also be inferred from the comparisons of T_{min}, T_{max}, and K with other mealybug species. Those species with similar parameters should have similar distribution range within the same climatic zone (Trudgill et al. 2005). Two common species, *P. madeirensis* and *P. citri*, are distributed throughout most of the continental United States (Ben-Dov 1994). *M. hirsutus*, which has a higher T_{min} and lower K than *P. madeirensis* and *P. citri*, should have a smaller distribution range than these two species. The distribution range inferred from comparison of biological parameters among different species, in combination with the results of the predictive models (e.g., NAPPFAST), may provide a more realistic prediction of the potential distribution range of a pest species.

Development of female and male *M. hirsutus* seemed to respond differently at 30°C, with the females completed development in 33 d and the males in 28 d. The deceleration of female development might be intimately linked to the deterioration of host plant quality at high temperatures. The development of herbivorous insects is often limited by the availability of nitrogen, in forms of amino acids and proteins, in the host plant tissues (Mattson 1980, Scriber and Slansky 1981). At 30°C, although the hibiscus cuttings developed roots in the water provided, they senesced earlier than those maintained at lower temperatures. Senescing plant tissues often have lower cellular nitrogen content (Hörtensteiner and Feller 2002); thus, they may have provided less than optimal quality or nitrogen levels for the mealybugs' nymphal development. Female mealybugs therefore suffered a slower nymphal development. However, male nymphs stop feeding after constructing a test for third- and fourth-instar developments. As a result, the males were less affected by a reduction in host quality and were able to achieve a similar developmental rate as those at 25 and 27°C. This supposed reduction in host quality did not affect the survivorship of *M. hirsutus*. Without a quantitative measurement of the nitrogen content of the hibiscus cuttings in this study, the negative effects of reducing host quality on the development of female *M. hirsutus* remain speculative.

Virgin *M. hirsutus* did not reproduce in this study, which contradicted the apparent parthenogenetic reproduction reported by Serrano et al. (2001). In this study, mated *M. hirsutus* produced on average 260–300 eggs when reared on hibiscus cuttings at 20–27°C. Persad and Khan (2002) reported a per capita fecundity of 178 eggs within 8 d when reared on hibiscus plants at 27°C. Serrano and Lapointe (2002) obtained the highest mean fecundity when the females were reared on Japanese pumpkin (162 eggs) and the lowest on a meridic diet (59 eggs). Other reports of *M. hirsutus* fecundity varied greatly from 84 to 654 eggs as reported in Ghose (1972) and 386–540 eggs reported by Mani (1986). As was shown by Serrano and Lapointe (2002), the difference in fecundity of *M. hirsutus* in these reports was likely the result of different host plant species or food substrates.

Life table analysis suggested that *M. hirsutus* has an enormous potential to increase its population level within a short period of time. The temperatures of 25 and 27°C were more favorable for the development, survival, and reproduction of *M. hirsutus*. At these two constant temperatures, *M. hirsutus* was able to achieve a net reproductive rate (R_o) of >150 female progeny per female (♀/♀) and a generation time (T_G) of slightly >40 d. The R_o and T_G reported in this study were higher than those (15.51 ♀/♀ and 34.23 d, respectively) reported in Persad and Khan (2002). The estimated intrinsic rate of increase (r_m) at 25 and 27°C was 0.12 ♀/♀/d, which was more than twice the rates

achieved at 20°C and 1.5 times of that reported by Persad and Khan (2002) at 27°C. *M. hirsutus* reared at 27°C in this study doubled its population in 5.8 d, whereas Persad and Khan (2002) reported a DT of 8.8 d. The differences between the results of this study and that of Persad and Khan (2002) could be because of qualitative differences between hibiscus cuttings and whole plants.

The life table parameters of *M. hirsutus* fall within the range reported in *S. sacchari* and *P. ficus.* The values of the life table parameters of *M. hirsutus* and *S. sacchari* were maximized near their respective T_{opt} (28°C for *M. hirsutus* and 30.4°C for *S. sacchari*) and reduced above T_{opt}. At 27°C, R_o of *M. hirsutus* was 14 times higher, r_m was 2.8 times higher, λ was 1.1 times higher, and DT was 2.8 times shorter than those at 30°C. For *S. sacchari*, R_o at 30°C was 3.5 times higher, r_m was 1.5 times higher, λ was 1.1 times higher, and DT was 1.5 times shorter than those at 33°C (Rae and De'ath 1991). The relationship between life table parameters of *P. ficus* and temperature was more variable (Walton and Pringle 2005). The highest R_o and r_m and the shortest T_G of *P. ficus* were not found at 27°C (T_{opt} = 27.8°C) but at 20 or 25°C.

An understanding of the life history of *M. hirsutus* has important implications in its management. The mass rearing of *M. hirsutus* for the productions of its parasitoids and predators should be conducted at 25–27°C to take advantage of high developmental rate, low mortality rate, and high fecundity at these temperatures. A comparison of the life history parameters of the pest and its natural enemies is also helpful in selecting the most appropriate biological control agents: the natural enemies with the higher intrinsic rate of increase relative to those of the target pests should be the more effective candidate (Huffaker et al. 1976). By comparing the life history parameters of *M. hirsutus* from this study and the parameters of natural enemies presented in Persad and Khan (2002), we agreed with the conclusion of Persad and Khan (2002) that the parasitoid *A. kamali* (r_m = 0.33) and the ladybeetle *C. montrouzieri* (r_m = 0.14) would be able to suppress the mealybug populations. Such conclusions are supported by the reports that the biological control programs against *M. hirsutus* using combinations of *A. kamali*, *G. indica*, and *C. montrouzieri* have been very successful in the Caribbean (Kairo et al. 2000), southern California (Roltsch et al. 2006), and Florida (D. Amalin et al., unpublished data).

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