Host Acceptance, Suitability, and Effects of Host Deprivation on the West African Egg Parasitoid *Telenomus isis* (Hymenoptera: Scelionidae) Reared on East African Stemborers Under Varying Temperature and Relative Humidity Regimens

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ABSTRACT Scelionid egg parasitoids of *Telenomus* spp. have been shown to significantly affect noctuid stemborer populations and yields of maize in western Africa. One of them, *T. isis*, has never been reported from eastern Africa and was introduced into the laboratories of the International Centre of Insect Physiology and Ecology, Kenya. This study evaluates the biotic potential of *T. isis* using East African stemborers as hosts. Host acceptance was tested using 15 lepidopteran borer species. Only noctuid stemborers were accepted for oviposition by *T. isis*. *Sesamia calamistis* Hampson, *Sesamia nonagrioides* (Lefebvre), and *Busseola fusca* (Fuller) were further used to study the effect of host species, host age, duration of host deprivation, temperature, and humidity on the performance of the parasitoid. In contrast to sex ratio, developmental time, parasitism, and parasitoid emergence varied significantly with host species, and the former two decreased with the age of host eggs. Female longevity increased with duration of host deprivation, whereas average lifetime fecundity decreased, probably because of oocyte resorption. *T. isis* successfully developed between 18 and 32°C at both low (40–50%) and high (70–80%) relative humidity regimens, but temperature played a more critical role. Using the modified Logan model, the lower and upper temperature thresholds for development were estimated at 11.5 and 37.5°C, respectively, with an optimum at 30.5°C for both humidity regimens. Depending on temperature and relative humidity regimen, the intrinsic rate of increase (r_m) varied from 0.077 to 0.300, net reproductive rate (R_o) from 7.70 to 83.96, and generation time (G) from 11 to 38 d. The results of this study indicate that *T. isis* is likely to establish in eastern Africa.

KEY WORDS *Telenomus isis*, East African stemborer species, temperature and humidity requirements, life table, host acceptability and suitability

In sub-Saharan Africa, the most important insect pests of maize are lepidopteran stem and ear borers belonging to the families Noctuidae, Crambidae, and Pyralidae (Polaszek 1998). The importance of a species varies greatly with season, agroecozone, and region (Schulthess et al. 1997). In West Africa, the most commonly reported species are the pyralid *Eldana saccharina* Walker and the noctuids *Sesamia calamistis* Hampson and *Sesamia botanephaga* Tams and Bowden (Schulthess et al. 1997, Sétamou et al. 2000); the noctuid *Busseola fusca* (Fuller), although a minor species in the humid areas, is common in the northern Guinea and Sudan savannah where, together with *Sesamia poephaga* Tams and Bowden, it attacks sorghum (Harris 1962, Schulthess et al. 1997). In East and Southern Africa (ESA), *B. fusca* and the invasive crambid *Chilo partellus* (Swinhoe) are the economically most important stemborers, whereas *S. calamistis*, *Chilo*

orichalcociliellus Strand, and *E. saccharina* are minor species (Bonhof et al. 1997, Songa et al. 2001, Zhou et al. 2001). *C. partellus* predominates in areas <1,500 m above sea level, whereas *B. fusca* is the main species in the cool agroecozones (Seshu Reddy 1983, Zhou et al. 2002, Ong'amo et al. 2006). In addition, recent phylogeography studies by Sezonlin et al. (2006), Assefa et al. (2006), and Ong'amo et al. (2008) identified several distinct populations of *E. saccharina*, *S. calamistis*, and *B. fusca* that vary in host plant range and climatic requirements.

Various control strategies including pesticides, host plant resistance, and cultural techniques have been developed and tested, all with partial success (Sétamou et al. 1995, Schulthess and Ajala 1999, Ndemah and Schulthess 2002, Bruce et al. 2004, Ali et al. 2006, Songa et al. 2007). In the 1990s, the International Institute of Tropical Agriculture (IITA) in West Africa and the International Centre of Insect Physiology and Ecology (ICIPE) in East Africa put more emphasis on biological control. ICIPE has focused on classical biological control of the exotic *C. partellus* using the Asian braconid larval parasitoid *Cotesia flavipes* Cam-

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eron. *C. flavipes* was first released in the coastal area of Kenya in 1993, where it reduced *C. partellus* densities by >50% (Zhou et al. 2002, Jiang et al. 2006). IITA, however, has promoted the redistribution approach, i.e., the exchange of parasitoids and strains between the African regions (Schulthess et al. 1997). For example, in the 1990s, IITA introduced a strain of *C. sesamiae* (Cameron) from the coastal region of Kenya, reared at ICIPE, into Benin, where it became established on *S. calamistis;* the parasitoid was also recently released in Cameroon (Ndemah et al. 2007, Gounou et al. 2009).

Egg parasitoids are an important source of mortality because the pest is killed before it damages the crop (Temerak 1981). In Kenya and ESA as a whole, egg parasitism is generally low (Bruce et al. 2006, Okoth et al. 2006; unpublished data). In contrast, in Benin, egg parasitism by the scelionids *T. busseolae* Gahan and *T. isis* Polaszek has been reported to reach 95%, and several studies yielded a positive relationship between maize yields at harvest and egg parasitism during the vegetative stages of growth (Sétamou and Schulthess 1995; Schulthess et al. 2001; Ndemah et al. 2001a, 2003). *T. isis*, which is commonly obtained from eggs of noctuid stemborers in West Africa and Cameroon in Central Africa (Sétamou and Schulthess 1995, Moyal 1998, Ndemah et al. 2001a, Schulthess et al. 2001, Chabi-Olaye et al. 2006), has never been reported from eastern Africa (Polaszek 1998), and it has been proposed for release in ESA (Schulthess et al. 1997, Chabi-Olaye et al. 2001a, Agboka et al. 2002). The parasitoid was introduced into the containment facilities at ICIPE in 2003 for release against *B. fusca*.

Suitable climate and availability of suitable hosts have been acknowledged as a major contributing factor to the successful establishment of many biological control agents (Godfray and Waage 1991, Goolsby et al. 2005, Pilkington and Hoddle 2006). Detailed information on temperature requirements, host range, and interspecific competition for *T. isis* exist for West but not for East Africa (Chabi-Olaye et al. 2001a, b, 2004; Agboka et al. 2002; Fiaboe et al. 2003). Moreover, the effect of relative humidity, which in tropical countries varies greatly with season and which may affect the adult parasitoid directly and development of immatures indirectly (Willmer 1982, Gautman 1986), was not taken into consideration in West Africa. In this study, therefore, acceptability and suitability of the local stemborers that attack both crop and wild host species were tested. It is assumed that alternative insect hosts living on wild host plants help to perennate the natural parasitoid during the off-season when *B. fusca* diapauses in the larval stage. In addition, the effects of host age and host deprivation, as well as temperature and humidity on the bionomics of the parasitoid using the three most common stemborer hosts occurring in the regions, where *B. fusca* is the key pest of cereals, were assessed. These results will assist in optimizing timing of field releases and in the selection of optimal sites with presence of suitable host during both the cropping and off-season in the different climatic zones.

Materials and Methods

Identification and Rearing of Hosts and Parasitoids. All insects were reared at the Animal Rearing and Quarantine Unit (ARQU) of ICIPE in Nairobi. *Chilo partellus* and *C. orichalcociliellus* were reared on a diet developed by Ochieng et al. (1985), whereas *S. calamistis*, *E. saccharina*, and *B. fusca* were reared on artificial diet according to the method described by Onyango and Ochieng-Odero (1994). The noctuid stemborers collected from wild grasses from Eastern and Western Kenya were reared until adult emergence on artificial diet developed by Onyango and Ochieng-Odero (1994). The identification of stemborers from wild host plants was done by Pascal Moyal, CNRS, Gift, France. A colony of *T. isis* was established from *B. fusca* eggs that were collected in Benin and reared following the protocol developed by Chabi-Olaye et al. (1997) for rearing of *T. busseolae*. Except for experiments on varying temperature and relative humidity, all the experiments including mass rearing were conducted at $25 \pm 1°C$, $70 \pm 5\%$ RH, and 12-L: 12-D photoperiod.

Host Species Acceptance. Host acceptance was considered as the ability of *T. isis* to parasitize the eggs of the 12 stemborer species tested. Behavioral events leading to successful oviposition by *T. isis* were described by Agboka et al. (2002). The same events were used to characterize successful oviposition by *T. isis* in this study. Five newly emerged couples for each of the 15-stemborer species were released in separate oviposition cages of 50 by 30 by 30 cm containing two 3-wk-old potted maize plants, except for *Eldana saccharina* for which tasseling maize plants (Atachi et al. 2005) were offered in 150 by 50 by 50-cm cages. A piece of cotton wool soaked in 5% sugar solution was added in a petri dish (5 by 2 cm) as a food source for the adults. Each stemborer species was allowed to oviposit until death of the female, and each egg in a batch was mapped to facilitate observation of host acceptance. Mated, 12- to 16-h-old, naïve females of *T. isis* (female without any oviposition experience) were used in this experiment. Because *T. isis* is proovigenic, the mating mostly takes place immediately after emergence. However, to ensure mating, virgin males and females were kept together for 2 h. One *T. isis* female was individually offered one fresh egg batch of ≈50 eggs collected from the maize plants during a 6-h period, on leaf sheaths. The experiment was discontinued if the female did not attack the egg batch after 20 min (Agboka et al. 2002). If the parasitoid attacked, the experiment was terminated once the parasitoid left the egg batch and did not return to the batch after 20 min (Agboka et al. 2002). The females were removed and eggs were incubated at $25 \pm 1°C$, $70 \pm 5\%$ RH, and 12-L: 12-D photoperiod until *T. isis* emerged. A completely random design with 30 replications for each borer species was used. Percentage of parasitism and progeny was recorded for each host species. Eggs were considered to be parasitized when they turned black (Flanders 1937).

Suitability of Host Age. Laboratory colonies of the most common noctuid stemborers *B. fusca*, *S. calamistis*, and *S. nonagrioides* were established and used in the subsequent experiments. Establishment of stable laboratory colonies of the other species failed. Fifty eggs of four age categories (i.e., 1, 2, 3, or 4 d old) were exposed to a <1-d-old naïve mated *T. isis* in a glass vial (2.5 by 7.5 cm). After 6 h, the female parasitoids were removed and exposed eggs were incubated at 25 ± 1°C, 70 ± 5% RH, and a 12-L:12-D photoperiod. Data on percentage parasitism, number of progeny, F_1 sex ratio (as the proportion of females), and preimaginal developmental time were collected. After 4 wk, stemborer eggs, from which neither parasitoids nor host larvae emerged, were dissected to determine death of parasitoids or host larva. Each treatment (host age) was replicated 15 times in a completely randomized design.

Effect of Host Deprivation on the Reproductive Potential of *T. isis*. Less than 1-d-old mated adult parasitoids were fed a 20:80 honey:water solution and left without hosts for 0, 2, 4, 6, 8, 10, 12, and 14 d. From each of these groups, 15 females were isolated individually in glass vials (2.5 by 7.5 cm), and eggs of *B. fusca*, *S. calamistis* and *S. nonagrioides* were offered daily ad libitum until death of the parasitoid. A completely randomized design was used. The eggs were transferred to a new vial every day and incubated at 25 ± 1°C, 70 ± 5% RH, and a 12-L:12-D photoperiod. Female longevity, number of parasitized eggs (eggs that turn black after 10 d), number of progeny, and F_1 sex ratio (as proportion of females) were determined for each noctuid species.

Effect of Different Temperature and Relative Humidity Regimens on the Bionomics of *T. isis*. The effect of eight constant temperature regimens (15, 18, 21, 24, 27, 30, 32, and 35°C) and two relative humidity regimens (40–50 and 70–80%) on the developmental rate of T. isis was tested using *B. fusca*, *S. calamistis*, and *S. nonagrioides* eggs as hosts. A batch of 50 1-d-old eggs were exposed to one naïve, mated *T. isis* female in a glass vial (2.5 by 7.5 cm). After 6 h of exposure at 25 ± 1°C and 70 ± 5% RH, eggs were removed and incubated under the eight temperatures and two relative humidity regimens until emergence of the progeny. The vials were placed inside rectangular acrylic cages (30 by 30 by 20 cm) with an opening on one side, which was sealed with a sliding door. Relative humidity in the cages was maintained at either 40–50 or 70–80%. Relative humidity was adjusted as per procedures described by Hodgman (1948). Salts were placed in a petri dish (90 by 25 mm). Calcium chloride was used to maintain 40–50% RH and ammonium chloride or cotton wool soaked with water for the 70–80% RH regimen. The cages were kept closed and sealed with petroleum jelly. A thermohygrometer was placed inside each cage to monitor both temperature and relative humidity. The two relative humidity regimens were maintained in two separate cages inside an incubator set at a particular temperature. Data on egg-to-adult development time and mortality (total number of emerged parasitoids/total number of host eggs that had been parasitized) for each species were recorded. Approximately 2–12 h after parasitoid emergence, 15 F_1 *T. isis* pairs per temperature and relative humidity treatment for each noctuid species were selected. A completely randomized design was used. Each parasitoid pair was placed in a separate vial (2.5 by 7.5 cm) and maintained at the same temperature and relative humidity, and honey was provided as a food source for the adult *T. isis*. One-day-old eggs of *B. fusca*, *S. calamistis*, and *S. nonagrioides* were introduced ad libitum into each vial. Every 24 h, new eggs were provided ad libitum, and each day the number of living females was recorded. The egg masses were maintained at the same temperature and humidity regimen and in the same experimental unit until F_2 adult *T. isis* emerged. Parasitism and F_2 parasitoids were counted, sexed, and their longevity, realized fecundity, number of progeny, and sex ratio were calculated for each temperature and humidity regimen.

Statistical Analysis. Data on parasitism, development time (d), total progeny per female, percentage of emergence, sex ratio, developmental time, and life table parameters at different temperatures and humidity regimens were subjected to analysis of variance (ANOVA), using the general linear model (GLM) procedure of SAS for PC (SAS Institute 1997). Percentage parasitism, sex ratio, total progeny per female, and mean of oviposition duration were separated using the Student-Newman-Keuls test, where ANOVA was significant, and the Dunnett test was done to compare the host deprivation treatments with the control.

Time from oviposition to emergence of adult parasitoid, survivorship rates, daily fecundity, and sex ratio at each experimental set were used to construct life tables from which demographic growth parameters were calculated. Only data from adult parasitoids that died naturally were used for calculation of demographic parameters, whereas those that got stuck in the honey solution or got entangled in the cotton wool were not used in the analysis. Life table statistics were calculated according to Hulting et al. (1990), using the Jackknife program. The preimaginal survivorship was calculated by dividing the number of individuals alive until adult eclosion by the number of eggs laid by each cohort. Difference in intrinsic rate of increase (r_m) values among populations were calculated following the protocol by Dixon (1987) and compared with Newman-Keuls sequential tests (Sokal and Rohlf 1995) based on Jackknife estimates of variance for r_m values (Meyer et al. 1986).

For estimation of the lower developmental threshold and the thermal constant ($K = 1/b$), i.e., the number of degree-days to complete the prereproduction phase, a regression over the linear range of the relationship between temperature (T) and developmental rates [$R(T)$] of the egg parasitoids was used (Campbell et al. 1974):

$$R(T) = a + bT \qquad [1]$$

For estimation of the lower and upper development threshold and the thermal constant, a modified Logan model (Logan et al. 1976) by Lactin et al. (1995) was used to describe the relationship between temperature and developmental rate:

$$R(T) = e^{pT} - e^{[pTmax - (Tmax - T)/\Delta]} + \lambda \qquad [2]$$

where T is the temperature (°C), and ρ, T_{max}, Δ, and λ are fitted coefficients.

The mode of Weibull (1951) was used to describe the relationship between temperature and realized fecundity of *T. isis*.

$$F(T) = (d_2/d_1) \times [(T - T_0)/d_1]^{(d_2 - 1)}$$
$$\times e^{\{-[(T - T_0)/d_1]d_2\} \times d_3} \qquad [3]$$

for *S. nonagrioides* as host and

$$F(T) = d_1 \times \left(\frac{d_3 - 1}{d_3}\right)^{\frac{1-d_1}{d_1}} \times \left[\left(\frac{T - T_0}{d_2}\right)\right.$$
$$\left. + \left(\frac{d_3 - 1}{d_3}\right)^{1/d_3}\right]^{d_1 - 1} e^{-\left[\left(\frac{T - T_0}{d_2}\right) + \left(\frac{d_3 - 1}{d_3}\right)^{1/d_1}\right]} + \frac{d_3 - 1}{d_3}$$
$$[4]$$

for *B. fusca* and *S. calamistis* as hosts.

$F(T)$ is the total oviposition, T_o is the lower temperature threshold for the model, and d_1, d_2, and d_3 are fitted coefficients.

All parameters in nonlinear models were estimated by minimization of the sum of squared residuals. Parameters were tested against 0 based on nonoverlap of 95% confidence intervals.

Results

Acceptance and Suitability of Host Species. *Telenomus isis* probed and oviposited in eggs of all the noctuid stemborers tested, including *B. fusca*, *Busseola phaia* Bowden, *S. calamistis*, *S. nonagrioides*, *S. oriaula* Tams and Boweden, *S. penniseti* Tams and Bowden, *S. poephaga*, *Sciomesa piscator* Fletcher, *Manga melanodonta* Hampson, *M. nubifera* Hampson, and *Sesamia* n. sp. 5 (Le Rü et al. 2006), but avoided eggs of crambid (*C. partellus*, *C. orichalcociliellus* Strand) and pyralid (*E. saccharina*) stemborers. The percentage of females ovipositing varied between 52.5% for *S. poephaga* to 97.0% for *S. calamistis* (Table 1). Parasitism was between 39.0% for *Sesamia* n sp. and 70.7% for *S. calamistis* ($F = 2.56$; df = 11,252; $P = 0.004$), whereas percentage parasitoid emergence ranged between 54.7% for *Sesamia* n sp. 5 and 90.7% for *S. nonagrioides* ($F = 2.56$; df = 11,252; $P = 0.004$).

Effect of Host Age on the Reproductive Potential of *T. isis*. There were significant differences in the parasitism, emergence, and developmental timebetween host species and host age (Table 2). Number of eggs parasitized (y) decreased linearly with host age (x) ($y = 61.5 - 4.3x$; $r^2 = 0.72$; $P < 0.0001$ for *B. fusca*, $y = 48.3 - 6.8x$; $r^2 = 0.92$; $P < 0.0001$ for *S. nonagrioides*, and $y = 57.8 - 7.9x$; $r^2 = 0.74$; $P < 0.0001$ for *S. calamistis*), and it tended to be highest with *B. fusca*

Table 1. Acceptability of eggs of several stemborer species and parasitism by female *T. isis* and percentage of emergence ± SE of parasitoid progeny

Host species	Females ovipositing (%)	Parasitism (%)	Emergence (%)
Noctuidae			
B. fusca	80.4 ± 6.16	64.8 ± 3.91a	85.0 ± 4.82ab
B. phaia	85.4 ± 6.16	61.8 ± 3.96ab	76.2 ± 4.47abc
S. calamistis	97.0 ± 7.42	70.7 ± 4.76a	88.0 ± 5.76a
S. cretica	82.5 ± 8.32	53.3 ± 4.39ab	60.8 ± 6.40bc
S. nonagrioides	72.7 ± 7.38	63.5 ± 5.07a	90.7 ± 4.47a
S. oriaula	85.0 ± 6.63	60.9 ± 6.41a	71.5 ± 6.44abc
S. penniseti	82.0 ± 7.42	55.0 ± 8.40ab	82.1 ± 6.44ab
S. poephaga	52.5 ± 8.31	55.8 ± 4.11ab	73.4 ± 6.59abc
Sci. piscator	78.7 ± 6.16	49.4 ± 3.91ab	87.2 ± 5.00ab
M. melanodonta	88.2 ± 8.31	47.1 ± 5.14ab	70.5 ± 5.90abc
M. nubifera	81.2 ± 7.38	52.3 ± 4.59ab	59.1 ± 7.40bc
Sesamia n. sp. 5	75.2 ± 8.96	39.0 ± 6.39b	54.7 ± 7.64c
Crambidae			
C. orichalcociliellus	—	—	—
C. partellus	—	—	—
Pyralidae			
E. saccharina Walker	—	—	—

Means within a column followed by the same lowercase letter(s) are not significantly different (SNK test; $P \leq 0.05$).
—, the parasitoid did not probe.

followed by *S. calamistis* and *S. nonagrioides* ($F = 14.6$; df = 2,44; $P < 0.0001$ for age 1; $F = 12.8$; df = 2,44; $P < 0.0001$ for age 2; $F = 19.80$; df = 2,44; $P < 0.0001$ for age 3; $F = 11.6$; df = 2,44; $P < 0.0001$ for age 4; Table 2).

Across host age, developmental time was shortest for parasitoids emerging from *Sesamia* spp. than *B. fusca* except for 4-d-old host eggs where *S. nonagrioides* produced the longest developmental time ($F = 23.2$; df = 2,43; $P < 0.0001$). With *S. nonagrioides* only, development time increased with host age ($F = 11.5$; df = 3,56; $P < 0.0001$). There was no clear pattern among host species, although with 1- to 3-d-old eggs, development timed tended to be greater with *B. fusca* as the host, whereas with 4-d-old eggs, it was longest with *S. nonagrioides* (Table 2). Sex ratios were always female biased, ranging between 0.62 and 0.77, and they did not vary with host age. It was higher with *B. fusca* than *S. nonagrioides* on 1-d-old eggs ($F = 2.38$; df = 4,52; $P = 0.0164$) and lower with *S. calamistis* than either *S. nonagrioides* and *B. fusca* on 4-d-old eggs (Table 2).

Effect of Host Deprivation on the Reproductive Potential of *T. isis*. Number of parasitized eggs tended to decrease with days of host deprivation but they did not vary from the control up to day 10 for *B. fusca* and day 12 for *Sesamia* spp. ($F = 5.70$; df = 7,119; $P < 0.0001$ for *B. fusca*; $F = 2.57$; df = 7,119; $P < 0.0001$ for *S. nonagrioides* and $F = 7.16$; df = 7,119; $P < 0.0001$ for *S. calamistis*), whereas the percentage of emergence of progeny remained the same until days 12, 10, and 10, respectively ($F = 5.21$; df = 7,119; $P < 0.0001$ for *B. fusca*; $F = 2.42$; df = 7,119; $P = 0.0242$ for *S. nonagrioides*, and $F = 5.43$; df = 7,119; $P < 0.0001$ for *S. calamistis*; Table 3). In most cases, number of parasitized eggs and number of progeny did not vary with

Table 2. Acceptance and suitability of eggs at four ages of three East African noctuid cereal stemborers to *T. isis*

Age (d)	B. fusca	S. nonagrioides	S. calamistis
Percent parasitism			
1	56.0 ± 2.10aA	41.3 ± 1.94aB	53.4 ± 2.25aA
2	55.4 ± 1.92aA	35.0 ± 3.20abB	39.9 ± 3.15bB
3	47.1 ± 1.69bA	28.1 ± 2.78bC	37.0 ± 1.81bB
4	44.4 ± 2.46bA	21.0 ± 3.27cC	31.1 ± 3.62cB
Emergence (%)			
1	93.4 ± 2.30aA	92.2 ± 6.61aA	82.1 ± 6.00aB
2	70.2 ± 5.64bB	89.9 ± 3.93a	75.1 ± 8.57aAB
3	67.2 ± 9.00bAB	62.2 ± 8.48bB	74.0 ± 7.48aA
4	57.9 ± 1.57b	56.6 ± 7.72b	53.7 ± 8.78b
Sex ratio			
1	0.77 ± 0.01A	0.66 ± 0.03B	0.74 ± 0.02AB
2	0.69 ± 0.02	0.69 ± 0.04	0.62 ± 0.05
3	0.68 ± 0.05	0.72 ± 0.02	0.70 ± 0.05
4	0.77 ± 0.01A	0.74 ± 0.04A	0.62 ± 0.03B
Egg-adult developmental time (d)			
1	20.7 ± 0.44A	18.1 ± 0.46cB	19.7 ± 0.50A
2	20.3 ± 0.52A	18.2 ± 0.36cB	19.0 ± 0.16B
3	19.8 ± 0.43A	19.6 ± 0.26bAB	18.5 ± 0.37B
4	19.4 ± 0.23B	21.0 ± 0.24aA	18.7 ± 0.20B

Means within column followed by the same lowercase letter(s) and means within rows followed by the same capital letter(s) were not significantly different (SNK test; $P < 0.05$).

host species and where significant they tended to be lower with *S. nonagrioides* than the other two host species. Percentage parasitoid emergence followed the same trend. There were significant differences between host species but there was no discernible trend. The host species × days of host deprivation interactions were significant ($F = 1.76$; df = 23,14; $P = 0.043$).

There was a linear relationship between longevity (*y*) and days of host deprivation (*x*) ($y = 8.6 + 0.71x$; $r^2 = 0.60$; $P < 0.0001$ for *B. fusca*; $y = 12.1 + 0.70x$; $r^2 = 0.57$; $P < 0.0001$ for *S. nonagrioides*, and $y = 14.6 + 0.56x$; $r^2 = 0.93$; $P < 0.0001$ for *S. calamistis*). Also, there

Table 3. Effect of host deprivation (d), numbers of eggs parasitized, and percentage of emergence of *T. isis* using eggs of three stemborers

Days	B. fusca	S. nonagrioides	S. calamistis
Number of parasitized eggs			
0	119.2 ± 1.71	94.6 ± 6.39	103.8 ± 8.63
2	121.8 ± 7.48a	92.5 ± 8.80b	102.4 ± 5.99ab
4	90.4 ± 6.86	84.8 ± 9.70	91.2 ± 7.30
6	91.0 ± 6.97	75.0 ± 7.76	80.9 ± 7.28
8	89.8 ± 8.71	68.6 ± 6.55	77.4 ± 7.37
10	81.4 ± 4.87[a]	70.4 ± 7.73	81.0 ± 1.27
12	80.4 ± 4.52[a]	63.9 ± 6.94[a]	68.8 ± 6.82[a]
14	71.2 ± 6.60[a]	62.6 ± 8.85[a]	56.8 ± 4.82[a]
Emergence (%)			
0	89.4 ± 1.85	78.9 ± 2.90	89.0 ± 2.83
2	81.3 ± 2.99a	77.7 ± 3.95b	89.3 ± 3.18a
4	81.1 ± 3.43	76.3 ± 3.31	86.1 ± 1.83
6	79.9 ± 3.93a	75.4 ± 2.98b	84.2 ± 2.81a
8	78.4 ± 2.81	73.0 ± 3.49	84.5 ± 3.51
10	76.8 ± 2.61b	72.6 ± 4.27b	79.7 ± 3.40a
12	76.2 ± 3.57b	69.4 ± 5.98[a]b	70.0 ± 3.43[a]a
14	73.9 ± 5.34[a]	60.9 ± 4.64[a]	75.1 ± 4.63[a]

Means within a row followed by the same lowercase letter are not significantly different (Student-Newmann-Keuls test; $P < 0.05$).

[a] Within a column, means are significantly different from the control (0 d of host deprivation; Dunnett one-tailed *t*-tests).

were linear relationships between days of host deprivation (*x*) and longevity (*y*) ($y = 8.6 + 0.71x$; $r^2 = 0.60$; $P < 0.0001$ for *B. fusca*; $y = 12.1 + 0.70x$; $r^2 = 0.57$; $P < 0.0001$ for *S. nonagrioides*, and $y = 14.6 + 0.56x$; $r^2 = 0.93$; $P < 0.0001$ for *S. calamistis*) and oviposition period ($y = 7.8 - 0.24x$; $r^2 = 0.53$; $P < 0.0001$ for *B. fusca*; $y = 9.3 - 0.20x$; $r^2 = 0.83$; $P = 0.05$ for *S. nonagrioides*; $y = 13.6 - 0.57x$; $r^2 = 0.92$; $P < 0.0001$ for *S. calamistis*). The oviposition period was negatively correlated with female longevity ($r = -0.62$; $n = 119$; $P = 0.013$ for *B. fusca*; $r = -0.65$; $n = 118$; $P < 0.0001$ for *S. nonagrioides*, and $r = -0.66$; $n = 118$; $P < 0.0001$ for *S. calamistis*). Sex ratios did not vary with treatment and were between 0.65 and 0.77. There were few significant differences among host species but without a discernible pattern, and the results are not shown here.

The intrinsic rate of increase (r_m) and net reproductive rate (R_o) decreased with days of host deprivation (Table 4). However, for r_m, there were no significant differences up to 6, 4, and 8 d of deprivation with *B. fusca*, *S. nonagrioides*, and *S. calamistis*, respectively; for R_o, significant differences were observed at and after 1 d with *B. fusca* and 6 d with both *Sesamia* species. There was no difference in the generation time (*G*) between deprivation treatments. However, it was higher for *S. nonagrioides* and *S. calamistis* than *B. fusca* with 2 d of host deprivation. The opposite trend was observed on day 8. At day 12, *B. fusca* and *S. calamisitis* had a higher generation time than *S. nonagrioides*.

Effect of Temperature and Humidity on the Survival and Developmental Rate of *T. isis*. For all hosts tested, and across relative humidity, *T. isis* did not completed development at 15 or 35°C; dissection showed that parasitoids died in the larval stage. The estimated lower temperatures supporting development at low and high relative humidity calculated by

Table 4. Life table statistics of *T. isis* females subjected to different periods of host deprivation (d) using eggs of three noctuid stemborers

Host deprivation	B. fusca	S. nonagrioides	S. calamistis
r_m, Jackknife estimate of the intrinsic rate of increase			
0	0.244 ± 0.003	0.237 ± 0.003	0.245 ± 0.004
2	0.241 ± 0.003	0.236 ± 0.005	0.245 ± 0.004
4	0.239 ± 0.003	0.231 ± 0.005	0.242 ± 0.004
6	0.235 ± 0.004A	0.212 ± 0.005[a]B	0.237 ± 0.005A
8	0.228 ± 0.005[a]A	0.213 ± 0.003[a]B	0.227 ± 0.005A
10	0.226 ± 0.003[a]A	0.208 ± 0.005[a]B	0.227 ± 0.008[a]A
12	0.220 ± 0.003[a]A	0.202 ± 0.007[a]B	0.227 ± 0.005[a]A
14	0.211 ± 0.004[a]	0.199 ± 0.007[a]	0.203 ± 0.005[a]
R_o, net reproductive rate			
0	73.5 ± 6.6	65.3 ± 3.9	68.7 ± 4.8
2	66.0 ± 4.0[a]	62.8 ± 4.9	67.4 ± 3.9
4	51.3 ± 3.3[a]	58.4 ± 5.2	59.5 ± 4.5
6	52.6 ± 4.2[a]	57.0 ± 3.8	59.5 ± 4.5
8	48.7 ± 3.7[a]	49.7 ± 3.9[a]	51.4 ± 4.8[a]
10	47.0 ± 2.8[a]	48.9 ± 5.1[a]	51.4 ± 4.4[a]
12	45.3 ± 2.5[a]	45.9 ± 4.0[a]	45.3 ± 4.4[a]
14	45.0 ± 4.2[a]	45.7 ± 5.3[a]	38.0 ± 3.2[a]
G, mean generation time (d)			
0	18.2 ± 0.308	18.0 ± 0.161	18.4 ± 0.178
2	17.6 ± 0.170B	18.3 ± 0.161A	18.1 ± 0.179A
4	18.7 ± 0.182	18.5 ± 0.223	18.8 ± 0.272
6	18.9 ± 0.326	18.2 ± 0.309	18.3 ± 0.113
8	18.9 ± 0.332A	17.8 ± 0.255B	18.0 ± 0.244
10	18.4 ± 0.133	17.8 ± 0.273	18.4 ± 0.212
12	18.4 ± 0.139A	17.7 ± 0.247B	18.6 ± 0.144A
14	18.8 ± 0.170	18.5 ± 0.205	18.5 ± 0.224

Means within a row followed by the same capital letter(s) are not significantly different (Student-Newman-Keuls sequential test; $P < 0.05$).
[a] Within a column, means are significantly different from the control (0 d of host deprivation).

equation 1 were 10.6 and 10.9°C for *B. fusca*, 10.4 and 11°C for *S. nonagrioides*, and 11.5 and 11.7 for *S. calamistis* [$R(T)_{low} = -0.03454 + 0.00321T$; $r^2 = 0.97$, $P < 0$ 0.0001 and $R(T)_{high} = -0.04152 + 0.00360T$; $r^2 = 0.97$; $P < 0.0001$ for *B. fusca*; $R(T)_{low} = -03167 + 0.00309T$; $r^2 = 0.97$; $P < 0.0001$ and $R(T)_{high} = -0.04231 + 0.00370T$; $r^2 = 0.98$; $P < 0.0001$ for *S. nonagrioides*; $R(T)_{low} = -0.03711 + 0.0347T$; $r^2 = 0.97$; $P < 0.0001$ and $R(T)_{high} = -0.03421 + 0.00320T$; $r^2 = 0.99$; $P < 0.0001$ *S. calamistis*). The thermal requirement to complete the prereproductive phase was 311 and 277 DD for *B. fusca*, 323 and 270 DD for *S. nonagrioides*, and 312 and 288 DD for *S. calamistis* at low and high relative humidity, respectively.

The modified Logan model gave a good fit to the data sets for all the three noctuid species and two humidity regimens (Fig. 1). The fitted parameters of the model were estimated for all the three stemborers. For *B. fusca*, $\rho = 0.00363$; $T_{max} = 42.8$; $\Delta = 2.5$; $\lambda = -1.04$; $r^2 = 0.67$; $P < 0.0001$ and $\rho = 0.00326$; $T_{max} = 41.0$; $\Delta = 2.1$; $\lambda = -1.04$; $r^2 = 0.67$; $P < 0.0001$ for high and low humidity, respectively. For *S. nonagrioides*, $\rho = 0.00352$; $T_{max} = 35.4$; $\Delta = 0.85$; $\lambda = -1.04$; $r^2 = 0.74$; $P < 0.0001$ and $\rho = 0.0030$; $T_{max} = 36.5$; $\Delta = 1.0480$; $\lambda = -1.03$; $r^2 = 0.75$; $P < 0.0001$, respectively, for high and low humidity regimens. For *S. calamistis*, $\rho = 0.0034$; $T_{max} = 42.8$; $\Delta = 2.38$; $\lambda = -1.038$; $r^2 = 0.67$; $P < 0.0001$ and $\rho = 0.0033$; $T_{max} = 41.5$; $\Delta = 2.21$; $\lambda = -1.04$; $r^2 = 0.66$; $P < 0.0001$, respectively, for high and low humidity regimens. Developmental time decreased and developmental rates increased with temperature (Fig. 1). The estimated lower temperature thresholds esti-

mated by the Logan model were similar to those calculated with equation 1. The optimum temperatures did not vary with relative humidity and they were 30.8°C for *B. fusca* and *S. calamistis* and 30.9°C for *S. nonagrioides*. The upper developmental thresholds were estimated at 33°C for *S. nonagrioides* and 36°C for *S. calamistis* and *B. fusca* (Fig. 1).

Parasitoid emergence was lowest at 18 and at 32°C and it was lower under the low than high relative humidity regimen (Fig. 2). With *B. fusca* and *S. nonagrioides*, the differences between relative humidity tended to be largest at the extreme temperatures of 18 and at 32°C, whereas with *S. calamistis*, they were similar throughout the entire temperature range. There were significant interactions between humidity regimens × temperatures ($F = 4.28$; df = 5; $P < 0.0008$), host species × temperatures ($F = 6.90$; df = 10; $P < 0.0001$), and host species × humidity regimens × temperatures ($F = 8.82$; df = 10; $P < 0.0001$), but not between host species × humidity regimens ($F = 1.38$; df = 2; $P = 0.2515$).

Longevity of *T. isis* females varied significantly with temperatures and humidity levels; it decreased with temperature and, in most cases, was lower in the low than high humidity regimen (Table 5).

Similar trends were observed for the oviposition period but significant differences among humidity regimens were only observed at temperatures >27°C for all three host species except for *S. calamistis*.

The relationship between numbers of parasitized eggs (i.e., total fecundity) and temperature was curvilinear (Fig. 3). With *B. fusca* and *S. nonagrioides* at
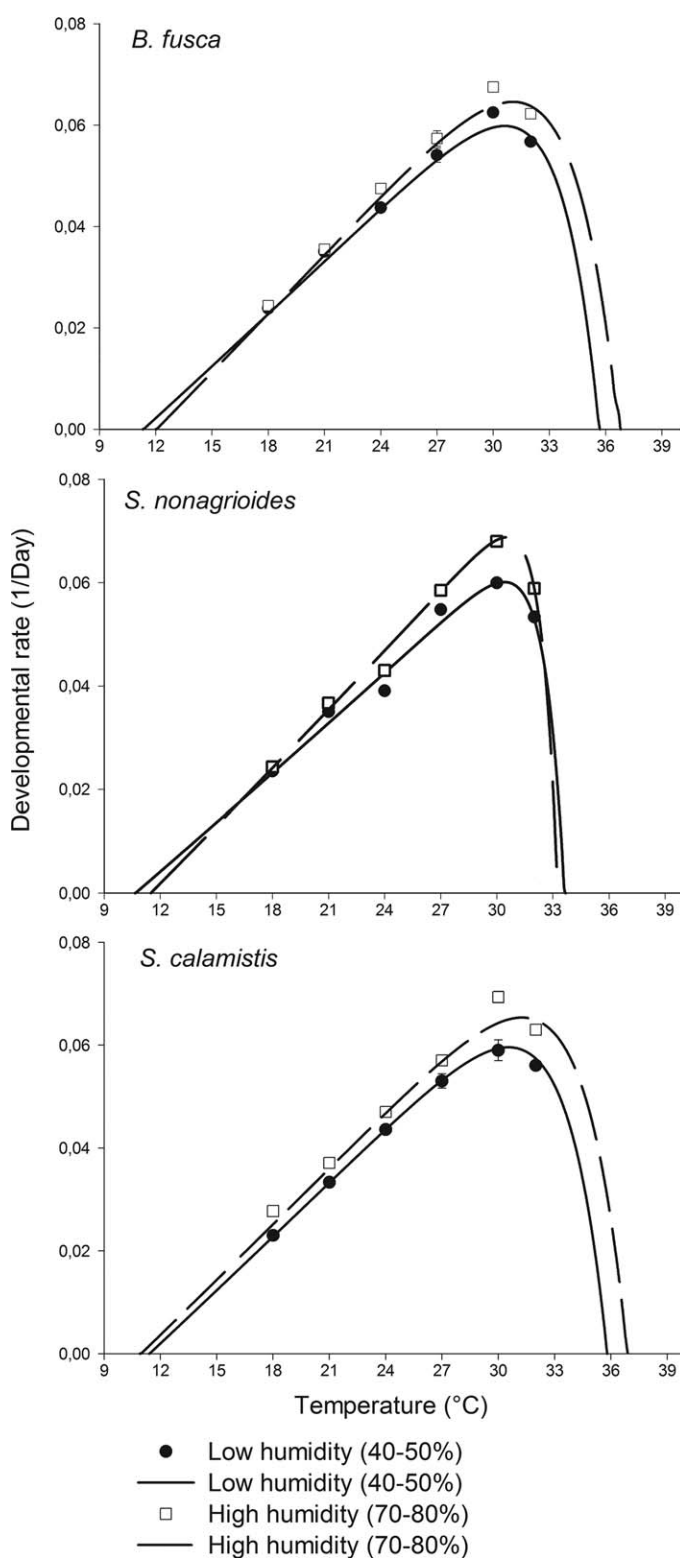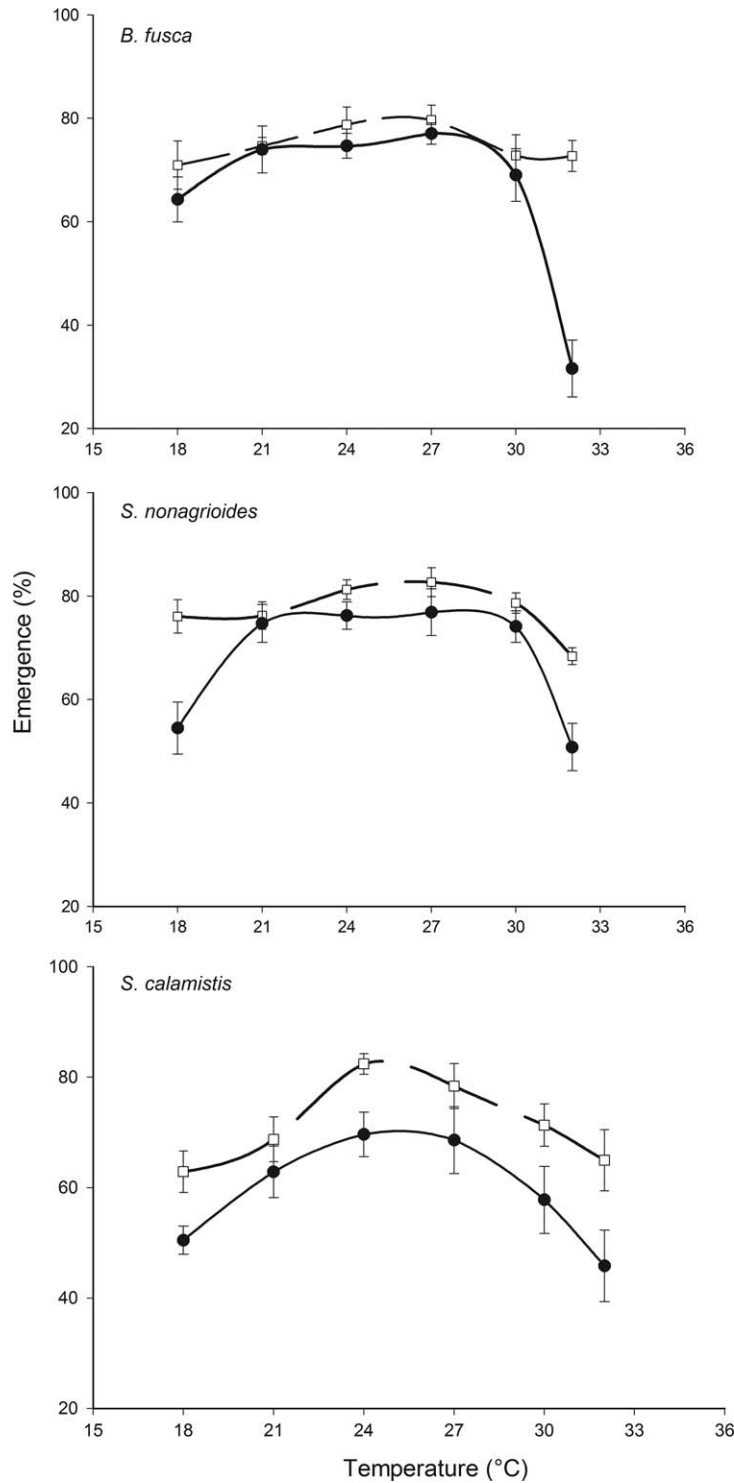
Fig. 1. Developmental rate of *T. isis* expressed as temperature (°C) function by use of the modified Logan model as describe by the Lactin et al. (1995) nonlinear function on eggs of *B. fusca, S. nonagrioides,* and *S. calamistis* at low (40–50%; ●) and high (70–80%; □) relative humidity.

Fig. 2. Emergence (%) of *T. isis* on eggs of three noctuid stemborers host at low (40–50%; ●) and high (70–80%; □) relative humidity.

both relative humidity regimens and with *S. calamistis* at the low relative humidity regimen, the optima were between 24 and 27°C, whereas for *S. calamistis* at high relative humidity, it was at 27°C. With *B. fusca*, the differences in fecundity tended to increase with temperature up to the optimum temperature and then

Table 5. Female adult longevity and oviposition time in days parasitism for *T. isis* on eggs of three noctuid stemborer species at different constant temperatures (°C) and two relative humidity regimens

Temperature	B. fusca		S. nonagrioides		S. calamistis	
	Low (40–50%)	High (70–80%)	Low (40–50%)	High (70–80%)	Low (40–50%)	High (70–80%)
Female longevity (d)						
18°C	$12.9 \pm 0.49aB^B$	$19.5 \pm 0.67aA^B$	$15.4 \pm 0.58aB^A$	$24.0 \pm 0.97aA^A$	$14.0 \pm 0.47aB^B$	$24.5 \pm 0.53aA^A$
21°C	$11.6 \pm 0.40abB$	$17.6 \pm 0.94aA^A$	$11.5 \pm 0.51bB$	$18.6 \pm 0.94bA^A$	$12.6 \pm 0.68a$	$13.4 \pm 0.28b^B$
24°C	$10.4 \pm 0.71bB$	$16.6 \pm 0.09aA$	$9.7 \pm 0.53cB$	$17.2 \pm 0.16bA$	$10.0 \pm 0.76bB$	$13.8 \pm 0.95bA$
27°C	$7.0 \pm 0.33cB^A$	$16.0 \pm 0.74aA^A$	$7.8 \pm 0.44dB^A$	$11.0 \pm 0.57cA^B$	$5.8 \pm 0.42cB^B$	$10.7 \pm 0.75cA^B$
30°C	$5.3 \pm 0.39dB^A$	$8.6 \pm 0.45bA^B$	$3.7 \pm 0.11eB^B$	$10.8 \pm 0.41cA^A$	$3.5 \pm 0.11dB^B$	$7.6 \pm 0.40dA^B$
32°C	$2.6 \pm 0.25eB^A$	$6.1 \pm 0.67cA^B$	$1.6 \pm 0.13fB^B$	$11.2 \pm 0.27cA^A$	$2.2 \pm 0.24eB^A$	$2.9 \pm 0.18eA^C$
Oviposition time (d)						
18°C	$10.3 \pm 0.31ab$	$9.0 \pm 0.80a$	$11.2 \pm 0.98a$	$8.4 \pm 0.86a$	$12.4 \pm 0.59a$	$17.3 \pm 0.50a$
21°C	$10.6 \pm 0.28a$	$9.2 \pm 0.97a^B$	$9.9 \pm 0.43a$	$8.3 \pm 0.39a^{AB}$	$11.4 \pm 0.83a$	$11.6 \pm 0.33ab^A$
24°C	$8.7 \pm 0.74b$	$8.5 \pm 0.30a^B$	$8.8 \pm 0.58a$	$8.3 \pm 0.28a^B$	$7.6 \pm 0.96b$	$9.1 \pm 0.62bc^A$
27°C	$6.6 \pm 0.39b^A$	$7.1 \pm 0.25a$	$6.9 \pm 0.38b^A$	$8.2 \pm 0.78a$	$4.2 \pm 0.50cB^B$	$7.4 \pm 0.82cA$
30°C	$4.0 \pm 0.46cB^A$	$6.6 \pm 0.52bA$	$3.2 \pm 0.18cB^{AB}$	$7.2 \pm 0.94aA$	$2.5 \pm 0.27dB^B$	$4.9 \pm 0.51dA$
32°C	$2.0 \pm 0.27dB$	$4.2 \pm 0.52cA$	$1.4 \pm 0.13dB$	$5.4 \pm 0.09bA$	$1.9 \pm 0.22d$	$2.5 \pm 0.21e$

Means within a column followed by the same lowercase letter(s), and means within a row followed the same capital or within row and host species followed by the same superscript capital letter(s) are not significantly different (SNK test; $P < 0.05$).

remained similar, whereas with *S. nonagrioides* and *S. calamistis* they increased up to 32°C. Overall, relative humidity had a more striking effect on fecundity with *S. calamistis* than the other two hosts. The Weibull (1951) model used to describe the fecundity of *T. isis* in relation to temperature and humidity gave a good fit for all hosts. For *B. fusca*, the fit of the model was $r^2 = 0.75$ and $P < 0.0001$; d_1 and d_2 were different from 0 ($P < 0.05$); they were $d_1 = 132.5$; $d_2 = 46.7$; and $d_3 = 7.9$ for high and $d_1 = 110.3$; $d_2 = 2078.5$; and $d_3 = 370.4$ for low humidity. For *S. calamistis*, the fit was $r^2 = 0.76$ and $P < 0.0001$, with d_1 and d_2 different from 0; they were $d_1 = 93.5$; $d_2 = 131.2$; and $d_3 = 18.6$ for high and $d_1 = 70.6$; $d_2 = 251920000$; and $d_3 = 40672471$ for low humidity. For *S. nonagrioides*, the model fit was $r^2 = 0.75$ and $P < 0.0001$, and d_1, d_2, and d_3 were significantly different from 0; they were $d_1 = 19.1$; $d_2 = 3.3$; and $d_3 = 1,914.9$ for high and $d_1 = 27.3$; $d_2 = 6.7$; and $d_3 = 1,276.8$ for low humidity (Fig. 3).

Sex ratios varied between 0.62 and 0.86. There were some significant differences among temperatures, with a slight trend of them being lower at the extreme than the moderate temperatures; where significant, they were higher in the high than low humidity regimen. However, there were few differences, and the data are not shown here.

At the low humidity regimen, the intrinsic rate of increase (r_m) was higher at 27°C for all host species than extreme temperatures such as 18 and 32°C, whereas at the high humidity regimen, it did not vary between 27 and 32°C for *B. fusca* and *S. calamistis* (Table 6). Similarly, the net reproductive rate (R_o) was higher at the intermediate than the extreme temperatures. Generation time (G) decreased with temperature.

Discussion

Telenomus isis attacked and developed in all noctuid species offered but refused to oviposit in eggs of crambid and pyralid borers. This corroborates results by

Chabi-Olaye et al. (2001a), who tested eggs of noctuid, pyralid, crambid, and tortricid stem and earborers, which attack cereals in West Africa. With the exceptions of *B. fusca* and *S. cretica*, the noctuids spend the dry season feeding on wild grasses and sedges (Le Rü et al. 2006). Thus, they may play an important role in maintaining *T. isis* populations when the target species *B. fusca* is diapausing in the larval stage. However, the diapause is facultative, and in areas with irrigated maize or in inland valleys in the humid forest zone, where maize is planted during the dry season, part of the *B. fusca* population may not diapause (Chabi-Olaye et al. 2006). Although per tiller densities of individual borer species on wild host plants are very low, the overall per area density can be considerable because, unlike maize, which does not tiller, wild host plants produce up to 40 tillers/m² (Ndemah et al. 2000, 2001b, 2002, 2007; Gounou and Schulthess 2004, 2009). In addition, as shown by Fiaboé et al. (2003) for *T. busseolae*, *T. isis*, and the trichogrammatid *Lathromeris ovicida* Risbec, egg parasitoids are attracted by the sex pheromones produced by the calling female *S. calamistis*. Many insect parasitoids use pheromones as long-range chemical cues that help to direct the parasitoid to areas where host mating is in progress or where oviposition has probably taken place (Vet and Dicke 1992, Godfray 1994). For *T. isis*, once the oviposition site is discovered, contact kairomones produced by the female moth are directly associated with the attack on host eggs (Chabi-Olaye et al. 2001b). This should considerably facilitate host finding and increase the chances of establishment of *T. isis* in ESA. Also, olfactometric studies showed that *T. isis* females responded to calling females of *B. fusca*, *S. nonagrioides*, and *S. calamistis* (Bruce 2008).

Telenomus isis successfully developed in 1- to 4-d-old stemborer eggs belonging to different borer species. However, similar to findings by Chabi-Olaye et al. (1997, 2001a, 2004) for *T. busseolae*, *T. isis*, and *L. ovicida*, and by Bruce et al. (2006) for the trichogrammatid *Trichogramma bournieri* Pintureau and Babault,
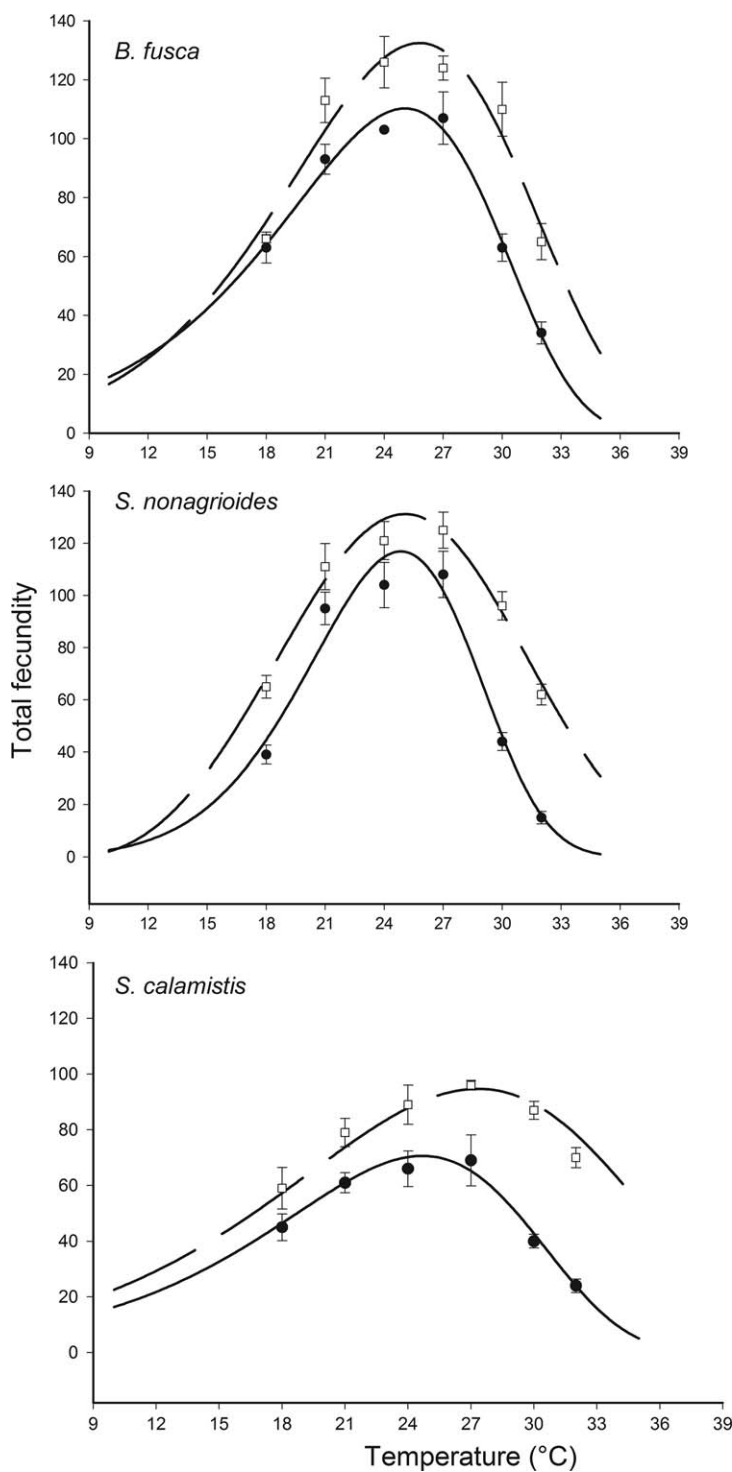
Fig. 3. Total fecundity of *T. isis* using *B. fusca*, *S. nonagrioides*, and *S. calamistis* expressed as a temperature (°C) function at low (40–50%; ●) and high (70–80%; □) relative humidity, using the Weibull model.

parasitism decreased linearly with host age. The lower suitability and preference of older eggs is common among egg parasitoids (Monje et al. 1999) and is prob- ably caused by hardening of the chorion, which makes it difficult for the parasitoid to probe (Safavi 1968). Generally, younger host eggs are parasitized more

Table 6. Life table statistics of *T. isis* on eggs of three different noctuid stemborer species reared at different constant temperatures and two relative humidity regimens

Temperature	B. fusca		S. nonagrioides		S. calamistis	
	Low (40–50%)	High (70–80%)	Low (40–50%)	High (70–80%)	Low (40–50%)	High (70–80%)
r_m, Jackknife estimate of the intrinsic rate of increase						
18°C	$0.086 \pm 0.002f^A$	$0.092 \pm 0.008d^B$	$0.077 \pm 0.002c^B$	$0.096 \pm 0.001e^A$	$0.080 \pm 0.002f^B$	$0.096 \pm 0.002d^A$
21°C	$0.149 \pm 0.002e^B$	$0.151 \pm 0.004c^A$	$0.165 \pm 0.003ab^A$	$0.178 \pm 0.004d^A$	$0.148 \pm 0.004e^B$	$0.144 \pm 0.002c^B$
24°C	$0.192 \pm 0.004cB^A$	$0.198 \pm 0.005ba^C$	$0.173 \pm 0.003a^B$	$0.218 \pm 0.006c^A$	$0.162 \pm 0.005c^C$	$0.199 \pm 0.003ba^B$
27°C	$0.279 \pm 0.005a$	$0.280 \pm 0.006a$	$0.252 \pm 0.004a$	$0.283 \pm 0.002a$	$0.285 \pm 0.009a$	$0.280 \pm 0.011a$
30°C	$0.247 \pm 0.005bB^A$	$0.289 \pm 0.005aa^A$	$0.206 \pm 0.004a^B$	$0.272 \pm 0.002ba^B$	$0.204 \pm 0.003bB^B$	$0.300 \pm 0.003aa^A$
32°C	$0.166 \pm 0.007dB^{AB}$	$0.273 \pm 0.006aa^{AB}$	$0.146 \pm 0.011bB^B$	$0.262 \pm 0.004ba^B$	$0.170 \pm 0.008dB^A$	$0.288 \pm 0.003aa^A$
R_o, net reproductive rate						
18°C	$28.56 \pm 2.38c^A$	$37.78 \pm 3.19c$	$18.44 \pm 1.74bB^B$	$35.92 \pm 2.20c^A$	$20.93 \pm 1.98bB^B$	$38.67 \pm 3.40b^A$
21°C	$45.06 \pm 2.45bB^A$	$55.37 \pm 3.19bA^A$	$46.93 \pm 3.10a^A$	$49.97 \pm 3.99b^{AB}$	$30.58 \pm 1.80a^B$	$48.01 \pm 2.21b^B$
24°C	$58.40 \pm 1.45a^A$	$73.69 \pm 1.31a^A$	$56.27 \pm 4.70ab^A$	$75.25 \pm 4.59a^A$	$34.18 \pm 3.44aB^B$	$51.49 \pm 4.09aa^B$
27°C	$56.65 \pm 4.72ab$	$65.96 \pm 2.16a^B$	$54.61 \pm 4.47aB$	$83.96 \pm 4.69aa^A$	$44.30 \pm 3.49a$	$51.44 \pm 4.36a^B$
30°C	$28.36 \pm 2.12cB^A$	$61.01 \pm 1.10abA^A$	$19.75 \pm 1.54bB^B$	$46.69 \pm 2.63ba^B$	$15.01 \pm 0.92cB^C$	$32.77 \pm 1.97bA^C$
32°C	$8.92 \pm 0.96dB$	$32.91 \pm 2.84cA^B$	$7.70 \pm 1.24cB$	$45.18 \pm 1.90ba^A$	$10.89 \pm 1.22dB$	$31.56 \pm 1.51bA^B$
G, mean generation time (d)						
18°C	$38.91 \pm 0.29a^A$	$37.47 \pm 0.67a$	$37.60 \pm 0.51a^B$	$37.31 \pm 0.39a$	$37.97 \pm 0.38a^{AB}$	$37.91 \pm 0.84a$
21°C	$25.47 \pm 0.17b^A$	$24.94 \pm 0.45b^A$	$23.22 \pm 0.14bA^B$	$21.95 \pm 0.33bB^B$	$22.99 \pm 0.28b^B$	$22.15 \pm 0.14b^A$
24°C	$21.19 \pm 0.30c^B$	$22.50 \pm 0.76c^A$	$23.18 \pm 0.39bA^A$	$19.80 \pm 0.62c^B$	$21.71 \pm 0.36c^A$	$19.80 \pm 0.23c^B$
27°C	$14.46 \pm 0.18d^C$	$14.91 \pm 0.33d^B$	$15.84 \pm 0.16c^B$	$15.61 \pm 0.23d^A$	$16.87 \pm 0.94dA^A$	$14.09 \pm 0.42dB^B$
30°C	$13.55 \pm 0.12f^B$	$13.30 \pm 0.42f^A$	$14.48 \pm 0.14e^A$	$14.08 \pm 0.18f^A$	$13.27 \pm 0.05fA^B$	$11.60 \pm 0.09fB^B$
32°C	$14.20 \pm 0.11eA^A$	$13.56 \pm 0.10eB^B$	$14.99 \pm 0.16dA^A$	$14.51 \pm 0.14eB^A$	$14.02 \pm 0.08eA^B$	$11.97 \pm 0.08eB^C$

Means within a column followed by the same lowercase letter(s), and means within a row followed the same capital or within row and host species followed by the same superscript capital letter(s) are not significantly different (SNK test; $P < 0.05$).

frequently than older ones (Hints and Andow 1990, Ruberson and Kring 1993). Pak (1986) hypothesized that rejection of old eggs could be attributed to either the rotation of host embryo or the sclerotization of the head capsule. The ability of an egg parasitoid to use different host egg stages is advantageous in times of host scarcity, when searching time may be prolonged. This is especially crucial in eastern Africa, where the cropping season is interrupted by a long dry season, when major pests such as *B. fusca* diapause in the larval stage (Zhou et al. 2001). Differences in parasitism among species in this study could be attributed to permeability, size, nutritional quality of host eggs (Waage 1986), and the duration of the egg stage, which for *B. fusca* is longer by 1 d compared with *Sesamia* spp. Also, studies by Honda and Luck (2000) indicated that embryological development among hosts varies between species, which might affect acceptability and suitability of a host.

Telenomus isis could be withheld from hosts for 8–10 d—depending on the host species—without parasitism being affected and with a concomitant increase in longevity. The decrease in total realized fecundity thereafter may be caused by both decreasing numbers of viable eggs and egg resorption. Similar results have been found for *T. isis* in West Africa with *S. calamistis* as the host, but in their study, parasitism started to decrease already at day 5 (Chabi-Olaye et al. 2001a). These findings support the trade-off hypothesis of negative correlation between reproduction and adult survival (Calow 1973, Browne 1982, Bell and Koufopanou 1986). According to Bell and Bohn (1975), egg resorption among insects is an adaptive

strategy, which allows females to conserve their metabolic resources instead of laying eggs under unfavorable conditions (Garcia et al. 2001).

In contrast to studies by Chabi-Olaye et al. (2001a) with *S. calamistis* as the host, parasitoids emerged at both 18 and 32°C with all three host species tested. Although the optimum temperature was similar, the minimum temperature was up to 3°C lower than the one calculated by Chabi-Olaye et al. (2001a), which cannot be explained by differences in relative humidity prevailing during the life table studies. The two laboratory colonies stemmed from the same area in Benin, but whereas the Benin colony was reared at 27°C, the Nairobi colony was kept at 25°C. Thus, an inadvertent selection of a population adapted to lower temperatures may have taken place. This is also corroborated by the successful emergence of parasitoids of the Nairobi colony at 18°C. Thus, the temperature range under which *T. isis* produced offspring was greater for the Nairobi than the Benin colony, indicating that it would adapt to a wider range of agroclimatic zones. In these studies, significant host species × temperature interactions were found for parasitoid emergence. Thus, differences in the host populations between West and East Africa may also influence the performance of the parasitoid.

Several authors have showed that, among physical factors, temperature exerts the strongest influence on the biological characteristics of egg parasitoids (van den Bosch and Messenger 1973, Noldus 1989, Dent 1991, Pratissoli 1995, Kalyebi et al. 2006), but optima, maxima, and minima differ among species and can have important consequences for parasitoid perfor-

mance. The optimum temperatures for development of *T. isis* in this study was ~30–31°C, which is similar to the one calculated for *T. isis* and *T. busseolae* in the lowland tropics in Benin (Chabi-Olaye et al. 1997, 2001a) and some trichogrammatids considered for augmentative releases against the African bollworm *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) in Kenya, which were tested under the same environmental conditions as *T. isis* in the current study (Kalyebi et al. 2005). Thus, although the lower and upper developmental threshold can vary considerable among these tropical species, the optimum temperatures are very similar. It is suggested that a change in overall temperature because of climate change would not affect the optimal temperature for development, but it might change the temperature range within which the insect could develop. However, the minimum temperature for development seems to be of little importance because, unlike in the temperate zones, in the tropics, mean minimum temperatures are usually well above the lower threshold calculated for these species. In fact, climatic modeling, which was used to predict the probability of establishment of *T. isis* in the different climatic zones, indicated that the 3°C shift in the lower temperature threshold observed in this study would not effect the distribution of *T. isis* in Africa (Bruce 2008). In contrast, an increase in the frequency of temperatures that exceed the extreme temperature tested in this study would directly (by lower fecundity and emergence rates) and indirectly (by premature induction of diapause in *B. fusca*, reduced availability of alternative hosts insects caused by reduced quality of host plant) affect the parasitoid and may cause local extinction.

Low relative humidity reduced both oviposition and parasitoid emergence, and thereby R_o, and increased G, both affecting r_m, whereby the effect was greater at the extreme temperatures (i.e., 18 and ≥30°C). Its extent was species specific as also indicated by the significant species × temperature × humidity interactions, except for 30°C, where emergence of *B. fusca* adults dropped drastically. With *S. calamistis* as the host, *T. isis* seemed to be more susceptible to low air humidity than with either *B. fusca* or *S. botanephaga*. Several authors have shown that parasitism by *T. isis* is low during the dry season, when temperatures are high and air humidity is low (Bosque-Pérez et al. 1994, Schulthess et al. 2001, Ndemah et al. 2003). This might be because of reduced host finding ability because the hosts feed on profusely tillering wild host plants that form dense stands, which reduces host finding by the parasitoid. Also, the rate of release of pheromones by the calling female moth that attracts the parasitoids may changes with temperature, and each parasitoid has its own optimal temperature for cue perception (Masuta et al. 2001, Reddy et al. 2002). Thus, according to Hance et al. (2007), extreme temperatures can affect the host–parasitoid population dynamics by altering the capacity of parasitoids to locate hosts and host habitats. In addition, desiccation of eggs may also affect emergence rates during the dry

season. The low parasitism at 18°C was probably caused by reduced parasitoid activity, and the low parasitoid emergence was a result of desiccation of eggs caused by a long development time of the immature parasitoid. The differences in emergence rate between host species might have been caused by the size of the host eggs; *B. fusca* has the largest eggs, followed by *S. nonagrioides* and *S. calamistis* (Bruce 2008). Larger eggs may have a thicker chorion, contain more water, and have lower surface area/volume ratios, and may therefore be less prone to desiccation.

Few studies have investigated the effect of relative humidity on the life history of parasitoids. For instance, mortality of immature and longevity of adult *Telenomus remus* Nixon decreased at 25% RH (Gautman 1986), whereas that of *Telenomus reynoldsi* Gordh and Coker was affected by relative humidity only at extreme temperatures (18 or 33°C) (Cave and Gaylor 1988). The physiological reason why developmental time increases at low relative humidity is not known but may be related to decreasing rates of feeding (Boudreaux 1958, Corbet 1968) or enzymatic reactions at suboptimal osmotic conditions. Willmer (1982) also suggested that evaporative cooling associated with transpiration could cause a decrease in body temperature with decreasing humidity, resulting in increased energy costs for maintaining water balance, and this may result in increased developmental time.

Based on the reproductive strategy, the high egg retention capacity, and an ability to successfully parasitize older eggs, Chabi-Olaye et al. (2001a) suggested that *T. busseolae* and *T. isis* have evolved in areas with strong environmental fluctuations. A comparison of the two *Telenomus* spp. showed that *T. busseolae* was much better adapted to long dry seasons than *T. isis*. *T. busseolae* was also reported from the pyralid *C. ignefusalis* in the Sahel (Youm 1990), whereas *T. isis* did not accept this species. It was proposed that *T. busseolae* was probably a savannah species, whereas *T. isis* seemed to have evolved in humid forest habitats, where the dry season lasts only 2–3 mo. This was verified by Chabi-Olaye et al. (2006), who found that, in the inland valleys in the humid forest zone in Cameroon, which are inundated during the rainy season but often planted with maize during the dry season, *T. isis* outcompeted *T. busseolae*, whereas in adjacent upland maize, it was the reverse. Thus, the best sites for first inoculative releases would be areas where suitable hosts are abundantly available all year round. Based on the present temperature studies, *T. isis* should establish in all agroecological zones. In the tropical highlands, however, mean temperatures during the main growing season can be as low as 17°C (Corbett and O'Brien 1997), and it is suggested that the parasitoid, even if it establishes, will not have much impact because of the low number of generations per year. Furthermore, in the zones from the lowlands to the dry mid-altitudes, the predominant borer species is *C. partellus*, followed by *S. calamistis* (Zhou et al. 2002). Thus, the zone, where *T. isis* would have the highest impact, should be the moist mid-

altitudes situated between 1,000 and 1,700 m above sea level. This is a high maize production zone, where *B. fusca* is the predominant pest, with bimodal distribution of rainfall, which allows for two crops per year. *T. isis* was released in Wundanyi in the moist mid-altitudes zones in southeastern Kenya in 2005. Recoveries were made in March and December 2006, validating the predictions by Chabi-Olaye et al. (2001a) and corroborating the results of this study. Unfortunately, no funds were available for 2007, but additional surveys will be carried out in 2008.

Telenomus isis was able to successfully develop in a number of insect hosts common in eastern African cereal systems and adjacent natural habitats and under a wide range of climatic conditions. Also, in situations of host scarcity, it was able to retain a high number of viable eggs, even if hosts were not available for 14 d. This suggests that *T. isis* will establish in ESA. Bionomic parameters and life table statistics, such as those presented in this study, provide a valuable tool in the evaluation of a potential biological control agent in an area that is climatically different to that of its native area (Bernal and Gonzalez 1997). This information will be used further in climatic models to produce maps of probability of establishment and possible impact of the parasitoid in the different agroecological zones in Africa, where *B. fusca* is of economic importance and *T. isis* is absent.

Acknowledgments

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