Factors Influencing the Developmental Rates and Reproductive Potentials of *Telenomus busseolae* (Gahan) [Hym.: Scelionidae], an Egg Parasitoid of *Sesamia calamistis* Hampson (Lep.: Noctuidae)

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The effect of seven constant temperatures on the development of *Telenomus busseolae* was determined, using *Sesamia calamistis* eggs as the host. The developmental threshold calculated was 13.7°C, the optimum temperature was 31°C, and the maximum temperature at which no parasitoid emergence occurred was 34°C. Female *T. busseolae* began ovipositing immediately after emergence. They produced more offspring during the first 24 h of adult life than during any subsequent period. At 20°C, adult females lived twice as long as those at 30°C (21.7 and 11.0 days, respectively). Total progeny of *T. busseolae* was significantly highest at 27°C. Mean fecundity ranged from 61 to 182 offspring per female. The effect of host age and host deprivation on the host parasitism rate, egg viability, and sex ratio of *T. busseolae* was also investigated. Only parasitism and emergence rates were affected by host age. The numbers of total progeny were the same between 0 and 10 days of host deprivation, whereas longevity tended to increase from 12.8 to 23.4 days from 0 to 14 days of withholding hosts. The percentage parasitoid emergence and the sex ratio were not affected by withholding hosts. *T. busseolae* is adapted to an ecosystem with strong environmental fluctuations that cause temporary scarcity of hosts and food. © 1997 Academic Press

KEY WORDS: *Telenomus busseolae*; *Sesamia calamistis*; life table statistics; temperature; host age; host deprivation; West Africa.

INTRODUCTION

Across Africa, the most serious insect pests of field-grown maize are lepidopteran stem and earborers belonging to the families Noctuidae and Pyralidae (Harris, 1962; Atkinson, 1980). In West Africa, *Sesamia calamistis* Hampson (Lep.: Noctuidae) and *Eldana saccharina* Walker (Lep.: Pyralidae) are the predominant species in areas with bimodal rainfall distribution (Bosque-Pérez and Mareck, 1990; Shanower *et al.,* 1991; Gounou *et al.,* 1994). Damaging population levels are usually reached on second season maize, between September and November. In the Republic of Benin, *S. calamistis* is the most abundant borer species but population densities usually are below injury level (Shanower *et al.,* 1991), although multiple cropping cycles of maize in southern Benin theoretically should cause serious yield losses in late planted maize. The reasons for these generally low *S. calamistis* densities in Benin are unknown. Recent studies (Chabi Olaye, 1992) and surveys (Sétamou and Schulthess, 1995) have shown that egg parasitism plays an important role. In southern Benin, the most common egg parasitoids are *Telenomus busseolae* (Gahan) followed by *T. isis* Polaszek [Hym.: Scelionidae], accounting for more than 90% of all species found. A survey in 65 farmers' fields in 1993 revealed an average rate of parasitism of 76.4% by both species. *Telenomus* spp. were shown to be one of the most important factors suppressing *S. calamistis* densities and reducing damage to the plant (Sétamou and Schulthess, 1995).

In subsaharan Africa, *T. busseolae* is frequently found associated with lepidopteran stemborers, and particularly *Sesamia* spp. and *Busseola fusca* Fuller (Lep.: Noctuidae) (Polaszek and Kimani, 1990). However, information on temporal and spatial distribution, as well as on the biotic potential, and thus importance, of this species are scarce. The present study was carried out to provide information on the bionomics of *T. busseolae* as affected by temperature, age of host eggs, and host deprivation to help to explain fluctuations in the population dynamics of this species in the field.

MATERIALS AND METHODS

Host and Parasitoid Culture

Larvae of *S. calamistis* were reared on ears of maize in the soft dough stage, in sterile plastic jars (13.6

length × 11.3 cm diameter). The ears were soaked in a 10% bleach solution for 15 min and then rinsed with sterilized water and dried with paper towel. Four ears with both ends cut off were placed in a jar with 200 1-day-old larvae. The ears were changed once a week, and on Week 2 the number of larvae per jar was reduced to 100. After 3 weeks pupae were extracted and transferred to oviposition cages for adult emergence. Moths were handled according to the method of Bosque-Pérez and Dabrowski (1989).

T. busseolae adults were obtained from a culture established at IITA Station, Benin. These parasitoids were obtained from collections in maize fields in southern Benin the same year and were reared on eggs of *S. calamistis* in transparent vials (11.6 length × 4.5 cm diameter) with honey streaked on the inside surface to provide food for adults. Fresh egg batches were supplied daily until death of adult *T. busseolae.* Because this parasitoid can easily be mistaken for *T. isis* Polaszek, specimens are frequently reidentified using the Polaszek *et al.* (1993) key.

Effect of Constant Temperatures on the Bionomics of T. busseolae

The effect of temperature on the developmental rate of *T. busseolae* was studied under eight constant temperatures: 15, 18, 20, 25, 27, 30, 32, and 34°C. Depending on temperature, the relative humidity ranged between 60 and 99%. Egg batches of 20 1-day-old eggs were exposed to one female parasitoid per treatment. Each treatment was replicated three times. After 6 h exposure, the eggs were transferred to new vials and kept under each selected temperature for incubation. The egg masses were observed twice daily until parasitoid emergence. Developmental time was determined from the end of the 6-h oviposition period to emergence.

For assessment of fecundity and longevity of adults, egg masses were exposed to parasitoids in incubators for 6 h at 20, 25, 27, and 30°C constant temperature. Approximately 2 h after parasitoid emergence, 20 pairs were selected per temperature treatment. Each pair was placed in a separate oviposition unit which contained batches of 100 1-day-old *S. calamistis* eggs (this stage and number of eggs were found to be adequate in a preliminary experiment) and honey. New eggs were provided every 24 h, and the number of *T. busseolae* females still alive was recorded daily until death. Exposed egg batches were held under the previously described temperatures until parasitoid emergence. Parasitoids were counted and sexed. Longevity and fecundity of adult parasitoids and sex ratio of offspring of *T. busseolae* were calculated for each specified temperature regime.

Effect of Host Age and Host Deprivation on the Reproductive Potential of T. busseolae

To determine the effect of host age on the reproductive potential of *T. busseolae,* 100 *S. calamistis* eggs of desired age (0, 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, or 5 days old) were exposed to previously mated females in transparent vials at 27 ± 1°C. Each treatment (host age level) was replicated 10 times. After 6 h exposure time, the eggs were transferred to new vials for incubation.

For the first host deprivation studies, adult parasitoids were kept with honey but without hosts for 2, 6, 10, 14, 20, and 30 days at 27 ± 1°C. Newly emerged and mated females were used as controls (0 days of host deprivation). From each of the seven groups, 10 mated females were individually isolated in transparent vials together with 100 host eggs. After 6 h exposure time, eggs were removed and transferred to an incubator.

In a second host deprivation study, adult parasitoids were kept with honey but without hosts for 0, 2, 6, 10, and 14 days at 27 ± 1°C. Mated females of the five age groups were individually isolated in transparent vials together with 100 host eggs. Every 24 h, old eggs were removed and incubated, and 100 new eggs were provided until death of the female. Each treatment was replicated 10 times.

The rate of parasitism was estimated as the number of emerged parasitoids plus clearly parasitized but unhatched eggs over total number of eggs exposed. Rate of emergence was determined by dividing the number of emerged adults by the number of visibly parasitized eggs. The sex ratio of the offspring was calculated as the proportion of females on total numbers of adults.

Statistical Analysis

The nonlinear model described by Logan *et al.* (1976) was used to predict development of *T. busseolae.* Hence, the relationship between the developmental rate per day $Z[T_c]$ and the temperature T_c is given by

$$Z[T_c] = p1\{e^{[p2(T_c - T_0)]} - e^{[p2(T_m - T_0) - 1/p3(T_m - T_c)]}\}, \qquad [1]$$

where T_0 is the lowest experimental temperature and T_m represents the maximum temperature at which no parasitoid emergence occurred in the present experiment. The parameters $p1$, $p2$, and $p3$ were estimated by Marquardt's (1963) nonlinear least squares technique using the SPSS program (Norusis, 1990). The calculation of the residual sum of squares was weighted with the number of individuals surviving at each temperature. The model was validated using development rates calculated for each temperature. The Logan *et al.* (1976) function has the advantage of being analytic over the entire range of temperatures and is described

TABLE 1

Mean Developmental Time (*T*), Longevity, and Oviposition Period in Days (d), Total Offspring per Female, and Sex Ratio of *T. busseolae* at Constant Temperatures

	Temperatures (°C)					
	18	20	25	27	30	32
T	42.7 ± 0.2a	33.3 ± 0.2b	17.3 ± 0.1c	15.7 ± 0.1d	12.2 ± 0.1e	12.5 ± 0.1e
Longevity (d)	—	21.7 ± 2.3a	12.9 ± 1.2b	12.8 ± 1.2b	11.0 ± 1.0b	—
Oviposition (d)	—	12.2 ± 1.2a	7.3 ± 0.7b	8.8 ± 0.8b	7.0 ± 0.6b	—
Total offspring	—	108.8 ± 6.2a	124.8 ± 8.4a	146.2 ± 4.7b	121.9 ± 5.6a	—
Sex ratio[a]	—	56.2 ± 1.1ab	58.1 ± 0.8a	45.5 ± 0.7ab	53.1 ± 1.3b	—

Note. (—) Not measured; means in a row followed by the same letter are not significantly different at $P \leq 0.05$ (Newman–Keul's test).
[a] Proportion of female progeny.

by parameters whose biological significance has been emphasized.

In addition, a simple regression over the linear range of the relationship between temperature (*T*) and developmental rates (1/development time) of *T. busseolae* was used to estimate the lower thermal threshold (T_0 = intercept/slope) and the thermal constant (K = 1/slope = the number of day-degrees to complete the prereproduction phase; Campbell *et al.,* 1974).

For parasitism, emergence, longevity, number of offspring, sex ratio, and duration of oviposition period analysis of variance (ANOVA) was used and means were separated by the Newman–Keul's test. Percentages were transformed to arcsin $\sqrt{p}$ before analysis. The significance level was set at $P = 0.05$.

From the temperature and second host deprivation experiment, net reproductive rate (R_0), generation time (G), and intrinsic rate of increase (r_m) were calculated after Birch (1948), with an algorithm provided by Prof. A. P. Gutierrez (University of California, Berkeley, personal communication). Time was expressed in days.

RESULTS

Effect of Temperature on Rate of Development

T. busseolae successfully completed development in the temperature range 18–32°C. No emergence occurred at 15 and 34°C, although dissection of eggs revealed fully developed parasitoids. Development time decreased linearly between 18 and 30°C, and ranged between 42.7 and 12.2 days (Table 1). The lower development threshold calculated via linear regression of developmental rate on temperature ($R(T) = -0.067 + 0.0049T$, $r^2 = 0.99$, $P = 0.0001$) was 13.7°C. Hence, the thermal requirement to complete the prereproductive phase was 204 day-degrees over a range of nonlimiting temperatures.

Following the above results, T_0 was chosen as 15°C and T_m as 34°C for the Logan *et al.* (1976) model. The

parameters *p*1, *p*2 and *p*3 of Eq. (1) were estimated as *p*1 = 0.017, *p*2 = 0.117, and *p*3 = 1.648, respectively with $r^2 = 0.99$, $P = 0.0001$ (Fig. 1). The optimal temperature for development was approximately 31°C.

Fecundity, Sex Ratio, and Longevity and Life Table Statistics

T. busseolae females began ovipositing on the first day of their emergence. They produced considerably more offspring during the first 24 h than during any subsequent period (Fig. 2). During the first 3 days of their life, *T. busseolae* females gave rise to more than 78% of the female progeny. The total number of offspring was highest at 27°C and similar in the other temperature treatments. The sex ratio (nontransformed) of the offspring ranged between 0.63 and 0.72 and was significantly lower (fewer females) at 30 than at 25°C. Mean longevity of ovipositing *T. busseolae* females ranged from 21.7 days at 20°C to 11.0 days at 30°C (Table 1) and was significantly lower at 30 and 25°C than at 20°C. In all treatments, the proportion of females produced decreased with age of ovipositing females (Fig. 2). The rates of decline increased with temperature.
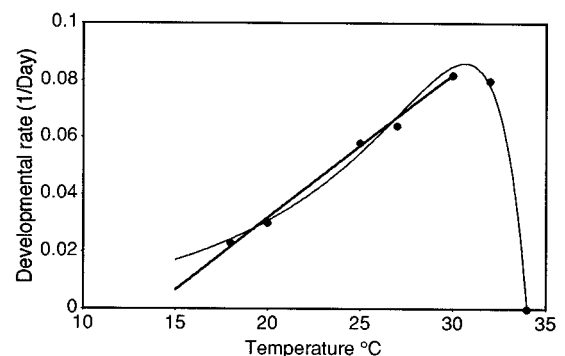

FIG. 1. The development rate of *T. busseolae,* expressed as a linear and nonlinear function of temperature (see text).
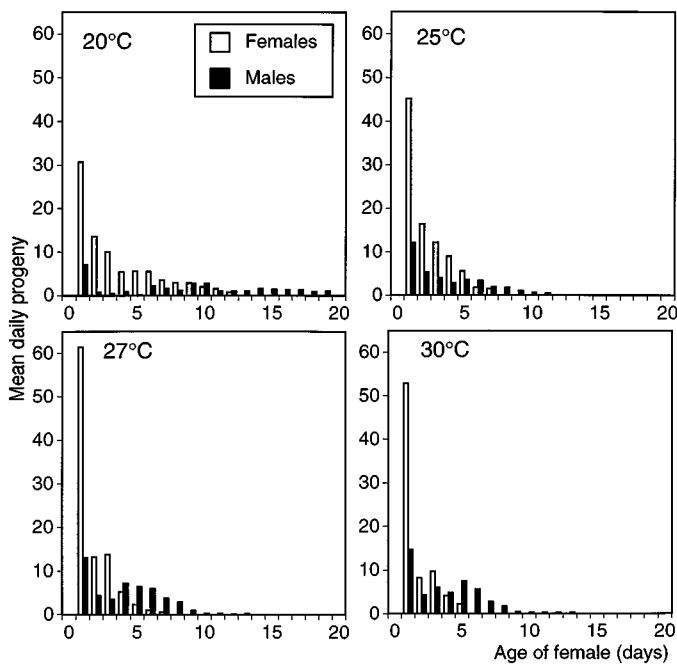
FIG. 2. Effect of four constant temperatures on mean daily progeny produced by *T. busseolae.*

The intrinsic rate of increase (r_m) increased and the generation time (G) decreased rapidly between 20 and 30°C, whereas the net reproductive rate (R_0) reached an optimum at 27°C (Table 2).

Parasitism and Life Table Statistics in Relation to Host Age and Host Deprivation

Rate of parasitism was similar on eggs between 0 and 2 days old ranging from 71 to 74% (nontransformed means from Table 3) and decreased linearly to 19% on 4.5-day-old eggs (arcsin $\sqrt{y} = -10.9\times + 79.9$, $r^2 = 0.90$, $P = 0.0001$). Five-day-old eggs yielded no parasitoids. Parasitoid emergence was slightly but significantly lower on 4.5-day-old eggs compared to the other treatments ($P = 0.01$) (Table 3), whereas sex ratio was not affected by host age.

In the first host deprivation experiment, where fe-male *T. busseolae* were allowed to parasitize for only 6 h, parasitism was similar between 0 and 10 days of host withholding, ranging from 71 to 75%, and afterward decreased linearly to 50% in the 30-day treatment (Table 4). The effect on percent emergence and sex ratio was not significant.

In the second experiment, where eggs were provided *ad libitum* during the entire life span of a female (after deprivation determined by treatment), numbers of total progeny were similar between 0 and 10 days of host deprivation and somewhat lower in the 14-day treatment (Table 5). Adult longevity increased in a linear manner from 12.8 to 23.4 days in the 0- and 14-day treatments, respectively. Parasitoid emergence and sex ratio was not affected by treatment.

As in the temperature trial, the highest proportion of offspring was produced on the first day in all treatments (Fig. 3). This was followed by a day of near 0 productivity, except in the 0-day treatment. Thereafter, cumulative numbers of offspring increased in a curvilinear manner and reached a plateau as the females grew older. A visual comparison revealed similar rates of production within the linear range for all treatments, but the maxima tended to decrease with days of host deprivation.

The intrinsic rates of increase (r_m) and net reproductive rates (R_0) decreased drastically by 65 and 78%, respectively, between the 0- and 14-day treatments, whereas generation time nearly doubled (Table 6).

DISCUSSION

The linear development rate model fitted the observations well only within the range 18 to 30°C, whereas Logan *et al.* (1976) described development of *T. busseolae* for the entire temperature range observed. During the growing season in southern Benin, daily mean temperatures ranged between 26 and 28°C. The highest means of around 30°C, i.e., the optimal temperature for development of *T. busseolae,* are observed mainly during the dry season, from December to February. During this period, maximum temperatures may reach 35°C for some hours a day. Temperatures below 20°C occasionally occur during nights in January. Thus, temperature should not be a limiting factor for the development of *T. busseolae* in this ecozone.

The thermal requirement (K) of 204 DD was considerably shorter than the 761 DD calculated for *S. calamistis* on maize, but T_0 was about 4°C lower for the latter (Shanower *et al.,* 1993a). However, at 25°C, for example, and depending on the nitrogen content of the plant (Sétamou *et al.,* 1993), r_ms and R_0s of *S. calamistis* feeding on maize were only 3–20% and 2–17%, respectively, of the values calculated for its parasitoid (Table 2). Thus, in terms of thermal requirement and

TABLE 2

Life Table Statistics of *T. busseolae* Reared at Various Constant Temperatures

	Temperatures (°C)			
	20	25	27	30
r_m	0.132	0.258	0.303	0.361
R_0	82.4	89.2	96.5	75.2
G	33.9	17.6	15.3	12.1

TABLE 3

Effect of Age of Host Egg on Parasitism and Percentage Emergence, and Sex Ratio of *T. busseolae*

	Host age (days)								
	0	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5
Parasitism	59.5 ± 0.7a	59.8 ± 1.1a	57.7 ± 0.6a	57.5 ± 0.9a	49.3 ± 0.7b	47.4 ± 0.6b	41.2 ± 1.2c	40.8 ± 0.8c	25.5 ± 1.8d
Emergence	88.4 ± 1.1a	89.1 ± 0.9a	89.4 ± 0.6a	90.0 ± 0.0a	88.5 ± 1.0a	90.0 ± 0.0a	90.0 ± 0.0a	89.1 ± 0.9a	84.8 ± 2.2b
Sex ratio[a]	0.8 ± 0.02	0.8 ± 0.01	0.8 ± 0.02	0.8 ± 0.02	0.8 ± 0.01	0.8 ± 0.02	0.8 ± 0.01	0.8 ± 0.02	0.8 ± 0.03

Note. Means in a row followed by the same letter are not significantly different at $P \leq 0.05$ (Newman–Keul's test).
[a] Untransformed data.

biotic potential, *T. busseolae* is considerably superior to its host *S. calamistis.*

Yeargan (1980) working with *Telenomus podisi* Ashmead noted that the time required for mating, searching, and oviposition are the main factors limiting the number of generations. *T. busseolae* males hatch first, wait on the egg batch for the females to emerge and immediately mate (Chabi Olaye, 1992). Thus, the time constraints for mating are negligible. The present data show that female *T. busseolae* are capable of ovipositing within hours after emergence, and if sufficient hosts are available (compare Tables 2, 3, and 5) lay more than half of their eggs within the first 6 h. Thus, during the first 3 days, a *T. busseolae* gave rise to about 78% of her female progeny. After that, the proportion of females dropped sharply. A similar trend in Scelionidae was recorded by Safavi (1968). The high rates of parasitism during the first 6 h of adult life indicated that emerging females already have many mature eggs. This pattern of egg laying corroborates the survey results by Sétamou and Schulthess (1995), who found that within egg batch parasitism averaged 94.5%, and about 57% of the egg batches collected in farmers' fields were completely parasitized.

Two other traits studied in the present work show that *T. busseolae* is a highly efficient parasitoid: it has the ability to successfully develop on late host stages and high egg retention capacity.

At 27°C the *S. calamistis* egg stage lasts about 6.5 days (Shanower *et al.,* 1993a). Thus, the present results show that *T. busseolae* is capable of developing on the host embryo during the later stages of host–egg incubation, although the suitability of 2- to 4.5-day host eggs decreased gradually by 50%. By contrast, *T. alsophilae* Viereck, an egg parasitoid of *Alsophila pometaria* (Harris), successfully parasitized only unembryonated eggs (Fedde, 1977).

The results of the host deprivation experiment showed that *T. busseolae* has a considerable egg retention capability. Withholding hosts for up to 10 days did not affect the parasitoids' reproductive potential but increased the longevity considerably. Thus, egg resorption was negligible. Viable eggs were stored in the ovaries of females which were as much as 30 days old. However, if hosts were withheld for more than 10 days, parasitism and total number of progeny decreased significantly due probably to both decreasing numbers of viable eggs and resorbtion or general loss of vigor of the aging females. These results are in contrast to the observations of Jubb and Watson (1971), who reported that *T. utahensis* oviposition did not occur if the female was 8 days or older.

High rates of parasitism by *T. busseolae* occur throughout the two cropping seasons on both maize and grasses, from April throughout October (Chabi Olaye, 1992; Schulthess, unpublished data). However, the reproductive strategy, the high egg retention capacity,

TABLE 4

Effect of Host Deprivation on Parasitism, Parasitoid Emergence (%), and Sex Ratio of *T. busseolae*

	No. of days of host deprivation						
	0	2	6	10	14	20	30
Parasitism	60.4 ± 1.1a	59.5 ± 1.1a	57.6 ± 1.0a	57.6 ± 0.7a	52.4 ± 0.9b	46.3 ± 0.9c	45.1 ± 1.0c
Emerged %[a]	99.6 ± 0.2	99.6 ± 0.1	99.8 ± 0.2	99.7 ± 0.3	99.8 ± 0.2	100.0 ± 0.0	99.3 ± 0.5
Sex-ratio[a]	0.80 ± 0.01	0.81 ± 0.01	0.79 ± 0.01	0.80 ± 0.02	0.79 ± 0.01	0.81 ± 0.02	0.78 ± 0.02

Note. Host eggs were exposed for 6 h. Means in a row followed by the same letter are not significantly different at $P \leq 0.05$ (Newman–Keuls test).
[a] Untransformed data.

TABLE 5

Effect of Host Deprivation on Mean Longevity and Ovipositional Period in Days (d), Percentage Emergence, and Total Progeny and their Sex Ratio of *T. busseolae* Subjected to Various Durations of Host Deprivation

	No. of days of host deprivation				
	0	2	6	10	14
Longevity (d)	12.8 ± 1.2a	14.4 ± 0.3a	18.4 ± 0.4b	21.6 ± 0.4c	23.4 ± 0.4d
Oviposition (d)	8.8 ± 0.8a	11.4 ± 0.4b	11.8 ± 0.4b	11.0 ± 0.4b	8.8 ± 1.5a
Emergence %[a]	99.5 ± 0.2	99.9 ± 0.1	99.8 ± 0.2	99.7 ± 0.3	99.8 ± 0.3
Total progeny	146.2 ± 4.7a	141.2 ± 4.0a	137.5 ± 5.7ab	135.0 ± 2.7ab	121.2 ± 6.3b
Sex ratio[a]	0.66 ± 0.01	0.64 ± 0.01	0.64 ± 0.02	0.63 ± 0.02	0.60 ± 0.02

Note. New host eggs were provided every day until death of parasitoid. Means in a row followed by the same letter are not significantly different at $P \le 0.05$ (Newman–Keul's test).

[a] Untransformed data.

and the ability to develop on old eggs show that *T. busseolae* is well adapted to an ecosystem with strong environmental fluctuations (see Stearns, 1976) that cause temporary scarcity of hosts and food. In the areas where the most common hosts, i.e., *Sesamia* spp. and the two diapausing species *B. fusca* and *Coniesta ignefusialis* (Hampson) (Lep.: Pyralidae), occur, the rainy season is interrupted by a 3- to 6-month period of drought. In southern Benin, the populations of *S. calamistis* start to decline during the second cropping season. The number of adults caught in light traps is close to 0 in December and remains low during the entire dry season (Kouamé, 1995). During the dry season, most of the female *S. calamistis* live on wild grasses, where juvenile mortality is above 95% (Shanower *et al.,* 1993b), and both pupal weight and fecundity are low because of the poor nutritional status of these hosts (Shanower *et al.,* 1993; Sétamou *et al.,* 1993). The other host of *T. busseolae* occurring in the area, *B. fusca,* diapauses as a larva mainly on old stems or crop residues. Field studies carried out in Nigeria

(Bosque-Pérez *et al.,* 1995) and Benin (Schulthess, unpublished data) show that *T. busseolae* is active during the entire dry season but parasitism is erratic and often low. During this period of scarcity of hosts, the reproduction of *T. busseolae* may be delayed for a long period after adult females emerge, which would have a drastic effect on the biotic potential of this species. Regression of life table parameters on days of deprivation showed that with each day of withholding hosts the intrinsic rate of increase and net reproductive rate decreased by 0.013 and 6.2, respectively. Also, because foods such as pollen and plant exudates are scarce during periods of drought, a high proportion of the eggs is probably resorbed. Thus, during the dry season, the biotic potential of this species may be severely reduced, resulting in the observed erratic and usually low parasitism.

The present work is part of a larger study on the feasibility of extending the geographic range of indigenous natural enemy species or strains in Africa for controlling cereal stemborers as proposed by several researchers (Mohyuddin and Greathead, 1970; Rao, 1965). *T. busseolae* was found across Africa, on various hosts such as *B. fusca, Sesamia* spp., and *C. ignefusialis* (Polaszek *et al.,* 1993). However, the occurrence and abundance of this parasitoid varies considerably with ecozone and region. The present study combined with
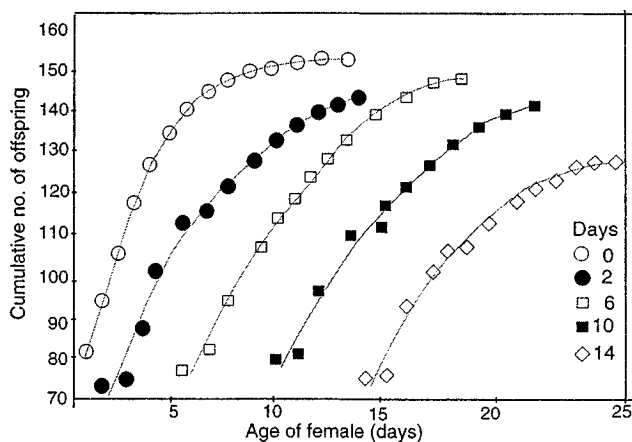

FIG. 3. Cumulative number of progeny of *T. busseolae* as affected by numbers of days of host deprivation.

TABLE 6

Life Table Statistics of *T. busseolae* Subjected to Varying Days of Host Deprivation

	Number of days of host deprivation				
	0	2	6	10	14
r_m	0.303	0.262	0.193	0.161	0.106
R_o	97.5	87.6	58.1	56.5	21.4
G	15.3	17.3	21.2	25.2	28.8

field studies in western and eastern Africa will help to elucidate the factors influencing the population dynamics of this species in the field.

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