Comparative studies on the effect of temperature on life tables of *Rastrococcus invadens* Williams (Homoptera : Pseudococcidae) and *Gyranusoidea tebygi* Noyes (Hymenoptera : Encrytidae)

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ABSTRACT

Laboratory studies of *Rastrococcus invadens* (host insect) and *Gyranusoidea tebygi* (parasitoid) were carried out at five constant temperatures of 20, 25, 30, 33, and 35 °C. Mango plant, *Mangifera indica*, was used as the host plant for *R. invadens.* A cohort of 20 larvipositing females was used at each temperature for both *R. invadens* and *G. tebygi.* The number of offsprings produced by each female and mortality within the cohort were recorded daily until all the members of the cohort had died. From these, fecundity and survival rate were calculated and used to construct the life tables of the two insects. The developmental period for *R. invadens* and *G. tebygi* increased with decrease in temperature from 20 to 33 °C. At 35 °C, the development of the male mealybugs was prevented beyond second instar, and females beyond first instar. The lower developmental temperatures for male and female *R. invadens* were 18.0 and 18.7 °C, respectively, while those for *G. tebygi* were 8.5 and 9.8 °C, respectively. Longevity and reproductive periods were inversely related to temperature for both insects. The optimum temperature for both insects was 30 °C. This was the temperature at which intrinsic rate of increase, total progeny, and net reproductive rate attained maximum values for *R. invadens* and *G. tebygi.* A comparison of the host-parasite relationship of *R. invadens* and *G. tebygi* showed that the parasitoid *G. tebygi* had a superior net reproductive rate, R^o, at higher temperature. At temperatures between 20 and 33 °C, *G. tebygi* had a higher intrinsic rate of increase than its host, *R. invadens.* It is suggested that *G. tebygi* can persist and increase in number over its host, and should be able to effectively control *R. invadens* at all the temperatures studied.

RÉSUMÉ

KEMABONTA, K. A. & ODEBIYI, J. A.: *Etudes comparées sur l'effet de température sur les tables biologiques de* Rastrococcus invadens *Williams (Homoptera: Pseudococcidae) et* Gyranusoidea tebygi *Noyes (Hymenoptera: Encrytidae).* Etudes de laboratoire de *Rastrococcus invadens* (insecte hôte) et *Gyranusoidea tebygi* (parasitoïde) se déroulaient à cinq températures constantes de 20, 25, 30, 33 et 35 °C. Le manguier, *Mangifera indica,* était utilisé comme la plante hôte pour *R. invadens.* Une cohorte de 20 femelles larvipostulates utilisées à chaque température pour *R. invadens* et *G. tebygi.* Nombre de progéniture produite par chaque femelle et la mortalité dans la cohorte étaient enregistrées tous les jours jusqu' à ce que tous les membres de la cohorte soient mort. De ces, la fécondité et la proportion de survie étaient calculée et utilisée pour construire les tables de vie de deux insectes. La période développementale pour *R. invadens* et *G. tebygi* augmentait avec une diminution en température de 20 à 33 °C. La température de 35 °C empêchait le développement de cochenille des serres au-delà de deuxième stade. Les faibles températures développementales pour le mâle et femelle de *R. invadens* étaient respectivement 18.0 et 18.7 °C, alors que celle de *G. tebygi* étaient respectivement 8.5 et 9.8 °C. Les périodes de longévité et de reproduction étaient inversement liées à la température pour les deux insectes. La temperature optimum pour les deux insectes était 30 °C. Ceci est la température à laquelle la proportion d'augmentation intrinsèque, la progéniture totale et la proportion reproductrice nette atteinaient les valeurs maximums pour *R. invadens* et *G. tebygi* qui montraient que le paracitoïde *G. tebygi* avait une proportion reproductrice nette supérieure, R^o, à une température plus élevée. A la température entre 20 et 33 °C, *G. tebygi*

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avait une proportion d'augmentation intrinsèque plus élevée que son hôte *R. invadens*. Il est suggéré que *G. tebygi* pourrait persister et augmenter en nombre plus de son hôte et devrait pourvoir contrôler efficacement *R. invadens* à toutes les températures étudiées.

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Introduction

The mango mealy bug, *Rastrococcus invadens* Williams was introduced into West Africa by accident between 1981 and 1982, where it became a major pest on many fruit trees such as mango, *Mangifera indica* (Anacardiacea) (Williams, 1986). The spread of the mealybug was a fast one, through Ghana and Togo in 1986 (Agunke *et al.*, 1988) to Côte d'Ivoire, Nigeria, and Zaire in 1988 (Neuenschwander, 1989).

R. invadens has been the most polyphagos pest of horticultural crops in West African countries since 1982. It is rated the most potentially dangerous pest (Mamman, 1989) and the second new dreadful enemy of horticulture (Wudil, 1989) in Nigeria. Moreover, in Nigeria, it has been recorded on about 33 plant species (Akinlosotu, Fajuyigbe & Anno-Nyako, 1988; Akinlosotu, 1989). Cultural, mechanical, and chemical control methods are likely to succeed with *R. invadens* control because of its polyphagy and rapid re-infestation of trees from host plant.

In 1989, the exotic parasitoid, *G. tebygi* Noyes, was released against *R. invadens* in Nigeria and since then, the parasitoid is well established and has been found in many areas where it was not released, with a high degree of synchronization with population fluctuation of its host (Hammond & Neuenschwander, 1990; Boavida, Neuenschwander & Schulthess, 1992; Boavida & Neuenschwander, 1995a; Gould, Bellows & Paine, 1992; Neuenschwander *et al.*, 1994; Matokot, Raid & Le Ru, 1992).

The rate of insect development depends upon the temperature to which the insects are exposed. To study the effectiveness of any parasitoid on a host insect, there is a need to know the threshold of development of the insect (Campbell *et al.*, 1974; Bursell, 1964). This is because the threshold of development may be a useful indicator of an insect's potential distribution and abundance (Messenger, 1970).

Not much work has been carried out on the effect of temperature on the development of *G. tebygi* on its host, *R. invadens*. This research, therefore, aimed at the following:

(i) To study the life table of the parasitoid, *G. tebygi*, and its host, *R. invadens*, at five constant temperatures.

(ii) To compare the life table parameters of the host, *R. invadens*, and that of the parasitoid, *G. tebygi*, to assess the effectiveness of the latter as a parasitoid on the former.

Materials and methods

Laboratory studies on the life tables of *R. invadens* and *G. tebygi* were conducted in experimental units placed in temperature cabinets (incubators) at constant temperatures of 20 °C (± 0.9), 25 °C (±1.1), 30 °C (±1.3), 33 °C (±1.9), and 35 °C (± 0.9).

Experimental unit

The experimental unit was a rectangular plastic container measuring 9.0 cm × 14.5 cm and 8.0 cm high. The four sides of the container were perforated with a hot 3-cm diameter iron rod to facilitate ventilation. The holes on three sides were covered with fine nylon mesh glued with evostick. A 2.5- cm wide test tube containing 20 ml of water was inserted through the bored hole on the fourth side. A leaf of mango plant was placed in the test tube and held in place at the petiole by cotton wool. The top of the plastic container was covered with a plastic lid to prevent the insects from escaping.

Culture cages

Ten wooden cages, each measuring 52 cm high in front, 59 cm high at the back, and 42 cm × 42 cm at the bottom and top, were used to culture *R. invadens* and *G. tebygi.* The slanted top was made of glass; the back and side panels comprised muslin cloth and the front was a wooden door. The door had two circular 12-cm diameter openings, each equipped with a sleeve made of white cotton materials to facilitate movement of materials in and out of the cage.

Culture of R. invadens

To ensure continuous and sufficient supply of all the developmental stages of *R. invadens* (host insect), its culture was maintained on potted seedlings of mango in the culture cages by transferring freshly collected lavipositing females from infested leaves in the field to the seedlings and removing them after lavipositing for 24 h. Mealy bugs that built up were used for subsequent experiments. (The males were not needed for culturing because from the preliminary studies carried out, the female mated only once in its lifetime and thereafter started to laviposit. Thus, already lavipositing females were used to start the culture of *R. invadens*).

Culture of G. tebygi

To ensure continuous and sufficient supply of *G. tebygi,* seedlings infested with 2nd-instar *R. invadens* were exposed to 120 male and female *G. tebygi* in the culture cage for 3 days. The parasitoids were removed thereafter and discarded, and the culture kept until the adults emerged. The 2nd instar of *R. invadens* was used because from the preliminary studies carried out, it was the most preferred host of *G. tebygi.*

Development and life table studies of R. invadens

Ten newly emerged 1st instar nymphs of *R. invadens* were each placed on a leaf below the apical shoot of a mango seedling and tagged (1 to 10). The procedure was replicated four times (five potted seedlings were used in each temperature cabinet). This procedure was repeated in the five temperature cabinets. The nymphs were observed daily for the exuvia, which was considered evidence of molting to the next stage. The developmental period from one stage to the other for *R. invadens* was noted. From this, the total developmental period was calculated.

A cohort of 20 newly larvipositing females was used for studies on the life table of *R. invadens.* One female each was placed on 20 mango leaves in an experimental unit in each temperature cabinet. This was replicated five times. The number of male and female offsprings produced by each female was counted daily and discarded. Mortality within the cohort was also recorded daily. This procedure was continued until all members of the cohort died.

Development and life table studies of G. tebygi

For *G. tebygi,* a cohort of 20-mated females was also studied at each temperature. A mango seedling infested with 20 3-day-old 2nd instars of *R. invadens* was exposed to each female daily for parasitization in an experimental unit at each test temperature. The mealy bugs were removed after 24 h and kept in the cages in the laboratory until they became mummified. The mummified mealy bugs were removed daily from the mango seedling, placed in gelatin capsules, and kept until adult *G. tebygi* emerged. The number of adults that emerged as well as mortality and survival levels among each cohort were recorded daily. This procedure was repeated until all members of the cohort had died. The number of adult parasitoids (male and female) emerging from each cohort and their developmental period were recorded.

Statistical analysis

The rate of development is the inverse of the duration in days (R) from birth to adult (for *R. invadens*), and from egg to adult (for *G. tebygi*). This was plotted against the rearing temperature. This relationship, according to Campbell *et al.* (1974) and Wigglesworth (1972), is described by the equation:

$$y = a + bT,$$

which gives the linear range of the relationship.

y is the y-axis,

T is the intercept of the regression line (temperature threshold), and

b is the slope of the regression line.

Life table studies

Daily survival (1x) and fecundity (mx) were used to construct the life tables on a format shown below, following the examples by Birch (1948) and Rae & De'art (1991).

x= Age of individuals in days (age interval column).

lx= The proportion of individuals still alive at age x.

mx= The number of female offsprings produced per female in the age interval x.

lxmx= The product of the 1x and mx columns for each age interval.

The following demographic parameters were calculated:

(i) Net reproductive rate (R^o): The average lifetime production of female progeny by an individual female in the cohort. It is calculated as the sum of 1xmx column.

(ii) Intrinsic rate of natural increase (r): The maximum rate of increase of a population under specified environmental conditions where food and space are unlimited. It was calculated from the equation:

$$r = \Sigma x^{-rx} 1xmx$$

Results

Developmental period of R. invadens *and* G. tebygi

For *R. invadens* (Table 1) and *G. tebygi* (Table 2), developmental period decreased as the temperature increased. However, at 30 and 33 °C, the periods for development for all stages were almost the same. Moreover, *G. tebygi* developed significantly faster than its host, *R. invadens*. Nymphs of *R. invadens* did not develop into adults at 35 °C. As a result, life table parameters could not be calculated for *R. invadens* and *G. tebygi* at 35 °C.

The total developmental periods for all stages of male (41 days) and female (43 days) *R. invadens* were significantly longer at 20 °C than at all other temperatures (25 – 33 °C) (Table 1). The shortest nymphal developmental period for *R. invadens* was recorded at 33 °C, but this was not significantly different ($P \leq 0.05$) from the developmental period at 30 °C. The developmental periods for all stages of male (27.2 days) and female (29.1 days) *G. tebygi* were significantly longest at

TABLE 1

Duration of Development (Days) for Different Stages of R. invadens *in Relation to Temperature*

	Male R. invadens				*Female* R. invadens			
Temp. (°C)	*1st instar*	*2nd instar*	*Pupal period*	*Total developmental period*	*1st instar*	*2nd instar*	*Pupal** period*	*Total developmental period*
20	$20.1 \pm 2.0^{a*}$	8.0 ± 1.5^{a}	12.1 ± 1.4^{a}	41.3 ± 1.6^{a}	20.1 ± 1.9^{a}	11.3 ± 1.61^{a}	11.9 ± 1.3^{a}	43.3 ± 2.5^{a}
25	15.5 ± 0.6^{b}	7.6 ± 1.2^{b}	12.0 ± 1.3^{a}	35.0 ± 1.3^{b}	14.9 ± 0.9^{b}	9.5 ± 0.9^{b}	9.5 ± 0.9^{b}	34.6 ± 1.3^{b}
30	8.8 ± 0.4^{c}	5.6 ± 0.9^{c}	9.5 ± 1.6^{b}	23.9 ± 1.1^{c}	8.8 ± 0.7^{c}	7.5 ± 0.76^{c}	7.9 ± 0.8^{c}	24.2 ± 0.9^{c}
33	8.8 ± 0.4^{c}	5.4 ± 0.7^{c}	8.8 ± 0.8^{b}	22.9 ± 0.9^{c}	8.2 ± 0.6^{c}	6.9 ± 0.9^{c}	7.9 ± 0.8^{c}	23.2 ± 0.9^{c}
35	7.3 ± 0.5^{d}	4.9 ± 0.4^{d}	ND***	ND	ND	ND	ND	ND

* Means followed by the same letter in each column do not differ significantly ($P = 0.05$) according to DMRT

** Values are means ± SD (in days)

*** Means no data (ND)

TABLE 2

Duration of Development (Days) for Different Stages of G. tebygi *in Relation to Temperature*

	*Life cycle of females**			*Life cycle of males**		
Temp. (°C)	*Total larval developmental period*	*Pupal period*	*Total developmental period (egg to adult)*	*Total larval developmental period*	*Pupal period*	*Total developmental period (egg to adult)*
20	18.2 ± 0.7^{a}	10.9 ± 1.1^{a}	29.1 ± 1.0^{a}	15.5 ± 1.2^{a}	10.8 ± 0.8^{a}	27.2 ± 0.6^{a}
25	16.0 ± 1.2^{b}	8.3 ± 1.3^{b}	24.4 ± 1.8^{b}	14.4 ± 1.1^{b}	7.9 ±2.2^{b}	22.9 ± 1.4^{b}
30	12.9 ± 1.3^{c}	7.6 ± 0.9^{b}	20.2 ± 2.0^{c}	11.6 ± 0.8^{c}	7.2 ± 0.7^{b}	18.9 ± 0.5^{c}
33	11.6 ± 0.9^{c}	8.2 ± 0.9^{b}	19.5 ± 0.7^{c}	10.8 ± 0.8^{c}	7.1 ± 0.6^{b}	17.9 ± 0.6^{c}

* Means followed by the same letter in each column are not significantly different ($P = 0.05$)
** Values are means ± SD (in days)

20 °C than at all other temperatures studied (Table 2).

Developmental temperature of R. invadens *and* G. tebygi

Irrespective of the sexes, the temperature threshold of development of *R. invadens* (nymphs) was higher than that of its parasitoid (egg to larva) (Fig. 1 and 2). The lower limits of temperature for the development of the male *R. invadens* and its parasitoid were 18.3 and 8.6 °C, respectively (Fig. 1), while those for the female were 18.5 and 9.5 °C (Fig. 2). In the host and the parasitoid, temperature threshold for the males was generally lower than that for the females.

Effect of temperature on longevity and reproduction of T. invadens *and* G. tebygi

An inverse relationship was recorded between temperature and longevity for *R. invadens* and *G. tebygi* (Table 3). However, *R. invadens* lived longer than *G. tebygi* at all temperatures tested.

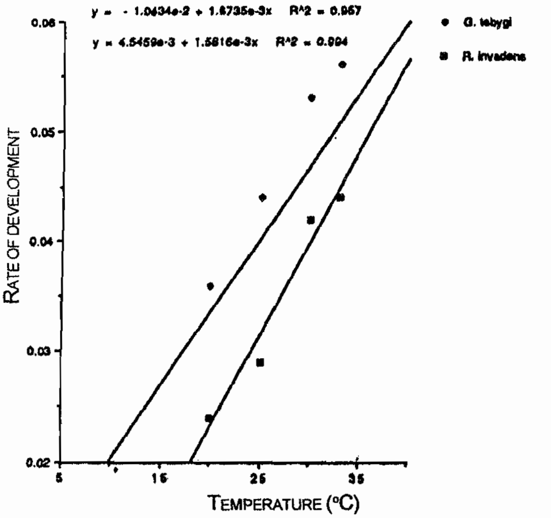

Fig. 1. Effect of temperature on the rate of development in *R. invadens* and *G. tebygi* males.

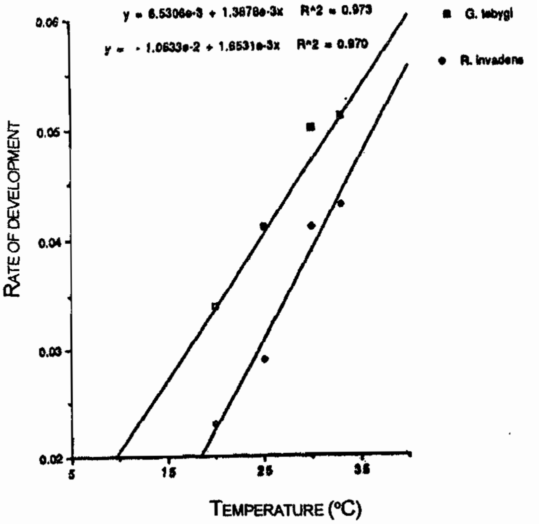

Fig. 2. Effect of temperature on the rate of development in *R. invadens* and *G. tebygi* females.

TABLE 3

Relationship Between Temperature, Longevity and Reproduction in R. invadens *and* G. tebygi

	R. invadens			G. tebygi		
Temp. (°C)	*Longevity (days)**	*Mean total progeny*	*Mean reproductive period*	*Longevity (days)*	*Mean total progeny*	*Mean reproductive period*
20	44.8 ± 5.1^{a}	83.1 ± 2.5^{c}	15.4 ± 3.3^{b}	20.1 ± 4.8^{a}	56.3 ± 3.9^{c}	17.7 ± 5.3^{a}
25	43.3 ± 1.9^{a}	124.7 ± 18.8^{b}	17.5 ± 8.0^{b}	21.5 ± 3.4^{a}	72.7 ± 11.0^{b}	19.9 ± 3.1
30	30.1 ± 2.6^{b}	205.0 ± 50.7^{a}	17.9 ± 2.3^{a}	20.7 ± 2.4^{a}	100.8 ± 19.8^{a}	18.0 ± 2.2^{a}
33	25.2 ± 2.2^{c}	127.3 ± 63.3^{b}	117 ± 3.3^{c}	15.3 ± 2.7^{b}	57.7 ± 10.2^{c}	12.8 ± 2.5^{b}

* Means followed by the same letter in each column do not differ significantly ($P = 0.005$) according to DMRT

** Values are means ± SD

The mean longevity of *R. invadens* at 33 °C (25.2 days) and 30 °C (31.1 days) were significantly lower ($P \leq 0.05$) than those at 20 °C (44.8 days) and 25 °C (43.3 days). The difference between the mean longevity of *R. invadens* at 20 and 25 °C was not significant. The mean longevity of *G. tebygi* ranged from 15.3 days at 33 °C to 21.5 days at 25 °C. *R. invadens* was active at 33 °C, but it remained motionless for a long period of time at 20 °C.

The maximum progeny production by the two insects (called optimum temperature for reproduction) was recorded at 30 °C. *R. invadens* was, however, significantly higher (205) ($P \leq 0.05$) than those at other temperatures (Table 3). Moreover, at 20 and 30 °C, an average of about 50 per cent increase in progeny production of *R. invadens* was recorded for every 5 °C rise in temperature. Similarly, more progeny was significantly ($P \leq 0.05$) produced by *G. tebygi* at 30 °C than at higher or lower temperatures (Table 3). Temperatures lower than 33 °C had no apparent significant effect on the reproductive period of *G. tebygi* (Table 3).

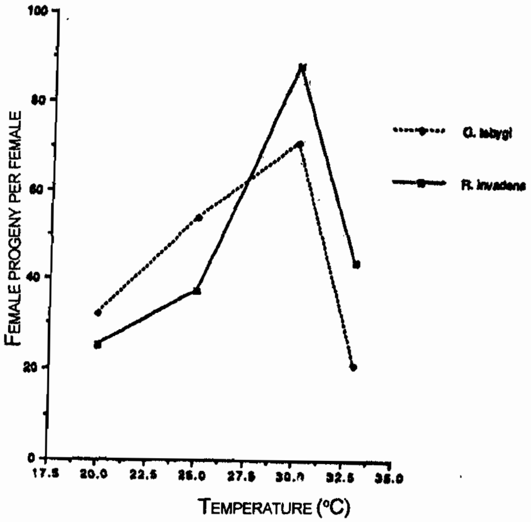

Fig. 3. Net reproductive rate of *R. invadens* and *G. tebygi.*

Net reproductive rate (R^{o}) and intrinsic rate of increase (r) of R. invadens *and* G. tebygi

The parasitoid, *G. tebygi*, had a superior ($P \leq 0.05$) fecundity at lower temperatures (20 and 25 °C) while the host, *R. invadens*, had a superior ($P \leq 0.05$) fecundity at higher temperatures of 30 and 33 °C (Fig. 3). Moreover, like the progeny production, the net reproductive ratio (R^{o}) reached the highest value at 30 °C in host and parasitoid.

At all temperatures (20 to 33 °C) tested, the parasitoid, *G. tebygi*, had a higher *r* than its host, *R. invadens* (Fig. 4). The intrinsic rate of increase increased gradually for the two insects to a peak at 30 °C and dropped, thereafter. The *r* in *G. tebygi* was highest (0.158) at 30 °C and lowest (0.108) at 20 °C.

Discussion

The difference in the total developmental period for the different nymphal stages of *G. tebygi* and

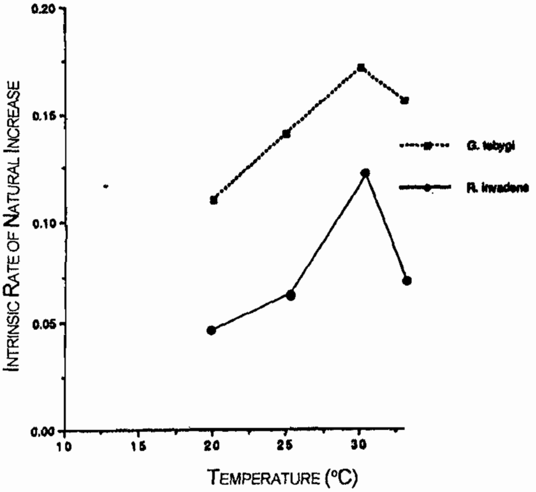

Fig. 4. Intrinsic rate of natural increase of *R. invadens* and *G. tebygi*.

R. invadens at 30 and 33 °C was not significant, indicating that higher temperatures were unfavourable for development. Although the upper temperature limit of development for *R. invadens* and *G. tebygi* were not established in this work, the fact that there was no development at 35 °C showed that the upper temperature limit for development was probably between 33 and 35 °C, since development was normal at 33 °C. *R. invadens* could not develop and survive at 35 °C. This might have resulted from various factors including protein denaturation and death at high temperatures resulting from dessication (Chapman, 1980).

The slow rate of development and the increased longevity in *R. invadens* at the lowest temperature (20 °C) may be because physiological activities are generally very slow at low temperatures. Thus, 20 °C is near the 18 °C developmental threshold of *R. invadens* established in this study. The optimal temperature for oviposition for *R. invadens* and *G. tebygi* was 30 °C. Thus, all reproductive parameters were optimal at this temperature. Fecundity of *R. invadens* at 33 °C (127) was lower than that at 30 °C (305), indicating that 33 °C was above the optimal temperature and close to its upper threshold temperature for oviposition.

At 30 °C, the value for r (0.124 for *R. invadens* and *G. tebygi*) was maximum, and the values for total progeny and net reproductivity rate were also maximum. It was also at 30 °C that the developmental period was shortest. Since the intrinsic rate of natural increase is greater than zero within the ranges of temperature studied, *R. invadens* and *G. tebygi* can persist and increase in numbers in these ranges (Birch, 1948; Chapman, 1980). The low value of r at 20 °C is probably due to the very long developmental period and the low R^{o} (net reproductive rate) at this temperature.

In this study, *R. invadens* and *G. tebygi* multiplied within 20 and 33 °C. However, in nature, the temperature range within which the species reproduce may be narrow, because 20 and 33 °C were hardly recorded over any appreciable length of time in the field, either during the day or at night (Kemabonta & Odebiyi, in press).

Moreover, the intrinsic rate of natural increase, though a reliable bio-climatic index, has limitations (Andrewatha & Birch, 1954). It is based on the assumption of unlimited food, space, and a stable age distribution. These conditions, however, depart from natural situations. Although the value of the intrinsic rate of increase, r, is affected by many other factors, it is still considered the most important factor affecting the distribution and the abundance of organisms (Messenger, 1970).

The developmental threshold of *R. invadens* was higher than that of its parasitoid. Therefore, the build-up of the parasitoid will not delay when the population of the host is low (Campbell *et al.*, 1974; Mackauer, 1972). Moreover, the net reproductive rate, R^{o}, of the parasitoid is superior to that of its host at lowest temperatures (20 and 25 °C). Therefore, the ability of the parasitoid to control the host at lower temperature will be enhanced. However, the higher value of the intrinsic rate of increase at all temperatures, and the faster developmental rate of *G. tebygi* over *R. invadens* suggest that *G. tebygi* can persist and increase in number over its host and should be able, at all the temperatures studied, to effectively control *R. invadens.*

Based on the research findings, *G. tebygi* appears to be an effective biological control agent against *R. invadens*. This result has been confirmed by other scientists (Boavida & Neueschwander, 1995b; Neuenschwander *et al.*, 1994).

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