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Resource allocation and bionomics of indigenous and exotic *Cotesia* (Hymenoptera: Braconidae) species reared on *Sesamia calamistis*

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Abstract

The braconid larval parasitoids *Cotesia chilonis* (Matsumura), *C. flavipes* Cameron and a strain of *Cotesia sesamiae* (Cameron) from coastal Kenya, reared at the International Centre of Insect Ecology and Physiology, were introduced at the International Institute of Tropical Agriculture in the Republic of Benin for suitability testing on West African stemborers prior to release. *C. chilonis* was originally collected in Japan while *C. flavipes* was imported into Kenya from Pakistan. The host species used was the noctuid *Sesamia calamistis* (Hampson), the most important noctuid maize pest in the region. All three *Cotesia* species attacked and successfully developed in 2nd to 6th larval instar of *S. calamistis* but parasitoid-induced mortality was highest on second instars. On most instars, *C. sesamiae* and *C. flavipes* produced larger broods than *C. chilonis*. Larvae parasitized by *C. sesamiae* developed to the 6th instar and attained an average larval weight of 353 mg, while larvae parasitized by *C. chilonis* only molted to the 4th instar and attained a maximum weight of 107 mg. The lower developmental threshold estimated from the non-linear regression of temperature on developmental rate was 15.9, 15.9 and 14.9°C for *C. chilonis*, *C. sesamiae* and *C. flavipes*, respectively, while the maximum temperature was 34.2, 35.2 and 33.8°C, respectively. A maximum of four ovipositions were observed per female during a life span ranging from 1.3 days for *C. chilonis* and *C. flavipes* to 1.6 days for *C. sesamiae*. The largest adult progeny, intrinsic rate of increase and net reproductive rates were recorded at 28°C for all species. However, across temperatures, *C. flavipes* yielded the highest number of offspring, followed by *C. sesamiae* and *C. chilonis*. The sex ratios did not vary significantly with species and temperature. Thus, the reproductive potentials of *C. sesamiae* and *C. flavipes* were greater than that of *C. chilonis*.

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Introduction

In West Africa, cereals are attacked by a complex of lepidoteran stemborers (Bosque-Pérez & Schulthess, 1998). While economic losses to rice and sorghum are rare, severe infestations occur on maize, particularly in areas with a bimodal rainfall distribution (Schulthess *et al.*, 1997a). Yield reductions of 10–70% due to the noctuid *Sesamia calamistis* Hampson and the pyralid *Eldana saccharina* (Walker) occur as a result of leaf feeding, stem tunnelling and direct damage to grain (Bosque-Pérez & Mareck, 1991; Cardwell *et al.*, 1997; Sétamou *et al.*, 2000; Chabi-Olaye *et al.*, 2005a). Losses are aggravated by poor soil fertility (Sétamou *et al.*, 1995; Chabi-Olaye *et al.*, 2005b).

Biological control (BC) of lepidopterous stem and cob borers has been proposed as a major component of integrated pest management (IPM) strategies in Africa (Greathead, 1971; Mohyuddin *et al.*, 1981; Mohyuddin, 1991). For the indigenous pest species, the exchange (or 'redistribution') of natural enemies between regions has been proposed (Rao, 1965; Schulthess *et al.*, 1997a) in addition to 'new association' BC, which entails the use of non-coevolved natural enemy species from closely related hosts occupying similar ecological niches in different geographic areas (Hokkanen & Pimentel, 1984; Schulthess *et al.*, 1997a). These approaches have led to the identification of several promising biocontrol candidates. For example, the braconid *Cotesia sesamiae* (Cameron) is the most common parasitoid of *B. fusca* and *S. calamistis* larvae in East and southern Africa (Greathead *et al.*, 1986; Kfir & Bell, 1993; Kfir, 1995, 1998; Zhou *et al.*, 2003). In contrast, in surveys in West African countries and Cameroon, *C. sesamiae* was very rarely found (Bosque-Pérez *et al.*, 1994; Moyal, 1998; Conlong, 2001; Ndemah *et al.*, 2001). It is not known if this is due to differences in host suitability. For example, in Kenya and Zimbabwe, *C. sesamiae* has been reported to exist as two biotypes, one of which sucessfully parasitizes both *B. fusca* and *S. calamistis* (virulent) while the eggs of the other are completely encapsulated in *B. fusca* (avirulent) (Ngi-Song *et al.*, 1998; Mochiah *et al.*, 2002; Chinwada *et al.*, 2003).

Three *Cotesia* species, the exotic *C. chilonis* (Matsumura) and *C. flavipes* Cameron and an avirulent coastal Kenyan strain of the native African *C. sesamiae*, were introduced from the International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya, into the laboratories of the International Institute of Tropical Agriculture (IITA) in Benin for suitability testing on West African stemborer species. Characteristics that determine whether biological control agents have an impact on the population dynamics of pests and make them efficient natural enemies for biological control programs have often been discussed (Doutt & DeBach, 1964; Waage & Greathead, 1998). In the present study, we investigated the resource allocation and bionomics of *C. chilonis*, *C. flavipes* and *C. sesamiae* using *S. calamistis* as host. More precisely, the study addressed the question of how much of the variation in parasitoid survival, brood size, sex ratio, developmental time and life table parameters could be explained by host size and quality.

Materials and methods

Parasitoid and host culture

The parasitoids were reared using *S. calamistis* as hosts. *S. calamistis* larvae were obtained from laboratory cultures maintained on artificial diet for 5–6 generations according to protocols described by Bosque-Pérez & Dabrowski (1989).

C. chilonis originated from field-collected *Chilo suppressalis* (Walker) (Lepidoptera: Crambidae) from rice, *Oryza sativa* L., in Niigata, Japan, that were transferred to ICIPE via Texas A&M University Entomology Quarantine (Okech & Overholt, 1996). *C. flavipes* originated from *C. partellus* on maize, in Rawalpindi, Pakistan (Overholt *et al.*, 1994). *C. sesamiae* was reared from *S. calamistis* collected on maize from the coastal zone of Kenya (Ngi-Song *et al.*, 1995). Prior to shipment to IITA, laboratory cultures of *C. chilonis* and *C. flavipes* were maintained on *C. partellus*, and *C. sesamiae* on *S. calamistis* at ICIPE for several generations. In Benin, all three parasitoids were cultured on *S. calamistis*. Larvae were allowed to feed and produce frass on fresh maize stem for 0.5 h prior to parasitoid exposure. Details of the parasitoid rearing protocol are as described by Ngi-Song *et al.* (1995).

Identification of host instar larvae and parameters used to characterize successful parasitism

Preliminary experiments showed that the parasitoids did not accept first instar larvae. Thus, 2nd through 6th instar larvae were used in the study. Larvae were harvested from the stock colony and sorted using size and head capsule widths to identify larval instars (Bonato & Schulthess, 1999). Each individual was weighed. Weight groups within an instar were selected and then individuals within an age group were chosen at random for experimental use (table 1). Selected larvae were maintained separately in Petri dishes.

To study the oviposition behaviour of *Cotesia* species and confirm successful parasitism, a hand-stinging method was used (Overholt *et al.*, 1994) in which 30 female parasitoids were transferred separately into transparent plastic Petri dishes (100 × 15 mm) arenas, and each offered a host larva for parasitism. Stung larvae were immediately removed and placed on an artificial diet for parasitoid development. Oviposition was considered successful when the *Cotesia* female inserted her ovipositor, raised her wings perpendicular to her body and the antennae were extended parallel to her body. Twenty-three hosts were dissected subsequently to exhibiting such behaviour by an ovipositing female. The behaviour was positive for parasitoid eggs in 97% of cases. This stereotyped parasitization behaviour and subsequent oviposition success were similar across parasitoid species. Thus, in subsequent experiments a host was considered 'parasitized' if the parasitoid expressed this behaviour.

Table 1. Age range and weight of 2nd to 6th instar of *Sesamia calamistis*.

Host instar	Age range (days)	Average weight (mg)	Confidence interval (95%)
Second	10–13	6.6	(5.7, 7.4)
Third	14–17	69	(65.6, 72.3)
Fourth	18–21	134.6	(129.9, 139.4)
Fifth	22–25	213.2	(209.5, 216.9)
Sixth	26–29	296.9	(290.4, 303.6)

Except for temperature-dependent survival and development, all experiments were conducted at 27 ± 1°C, 50–90% RH and a photoperiod of 12 : 12 (L : D).

Effect of host age on parasitoid survival, brood size, sex allocation and developmental time

Second to 6th instar larvae were offered individually for parasitism to a single, naïve, mated *Cotesia* female in a transparent Petri dish (10 cm height × 1.5 cm diameter). The host-parasitoid interaction was continuously observed for parasitism. Parasitized larvae were removed from the arena and individually reared in plastic vials containing an artificial diet. For each host age, 30–40 parasitized and 20 unparasitized larvae were reared. Data gathered were: % parasitized hosts that successfully produced parasitoid cocoons, % parasitized hosts that died, % parasitized hosts that pupated, % successfully emergent parasitoid adults, parasitoid brood size, sex ratio (% females in the total brood) and developmental time (days). Mortality was estimated as % hosts that died as larvae or pupae after being parasitized by a female parasitoid

Effect of parasitism on larval growth

This experiment was conducted with second instar larvae confined with either *C. chilonis* or *C. sesamiae*. Weights of parasitized and unparasitized second instar larvae were recorded at 0, 24, 48, 72, 120, 168, 216 and 264 h post parasitism. Thereafter, individual larvae were immediately transferred to a fresh artificial diet. Measurements were terminated when either the host pupated, died or parasitoid cocoons were produced.

Temperature dependent survival and development

The effect of constant temperature regimes (19, 25, 28, 30, 31, 32 and 34°C) on the developmental rates and survival of *C. chilonis*, *C. flavipes* and *C. sesamiae* were tested using fourth instar *S. calamistis* as hosts. For each temperature, the relative humidity varied between 50–90%.

A host larva was continuously observed for parasitization by each naïve, mated female of *Cotesia* species in a Petri dish (10 cm height × 1.5 cm diameter) at 28°C. Host larvae scored positive for parasitoid attack were transferred to a fresh artificial diet and randomly assigned to one of the seven constant temperature regimes. For each temperature regime, 50–65 parasitized and 30 unparasitized larvae were reared. Unparasitized larvae were used as a control to estimate the background mortality. Percentage of parasitized hosts that successfully produced parasitoid cocoons, % parasitized hosts that died, % parasitized hosts that pupated, % successfully emergent parasitoid adults, parasitoid brood size, sex ratio and egg-to-adult developmental time (days) were recorded. Data gathered on the egg-to-adult developmental time were used to estimate the lower developmental threshold for each *Cotesia* species and to describe the relationship between developmental rate and temperature.

Effect of constant temperature on the reproductive potential of three Cotesia *species*

Life table studies of *C. chilonis*, *C. flavipes* and *C. sesamiae* were carried out at four constant temperatures (19, 25, 28 and 30°C) using *S. calamistis* as the host. Naïve, mated parasitoid females were offered fourth instar larvae in a short tunnel bored into one end of a piece of maize stem with a 1 : 1 parasitoid to host ratio. Parasitism was expected when the frass was thrown out of the tunnel by the struggling larvae. Thereafter, larvae were removed and a new infested stem piece was offered until the parasitoid died. Parasitized larvae were reared on an artificial diet until the production of parasitoid cocoons or host pupae. Parasitoid females used for this experiment were continuously fed honey streaks in a plastic container (11.6 cm length × 4.6 cm diameter). The procedure was replicated four times with a cohort of 20 females for each parasitoid-host pairing. Female longevity was determined and for each parasitoid female, the total progeny produced was counted and sexed. Data gathered were used to compute the life table statistics of parasitoid species.

Statistical analyses

Differences in parasitism, developmental time, mortality, total progeny, sex ratio and life history parameters between host instar larvae, *Cotesia* species or temperature were analysed by analysis of variance (ANOVA) using the general linear model (GLM) procedure of SAS for PC (SAS Institute, 1989). Percentages were transformed to arcsine values before analysis. *F* statistics from type III sums of squares were used for tests of significance and means were separated using the Tukey test. The significance level was set at $P = 0.05$.

For estimation of the lower developmental threshold (T_0 = intercept/slope) and the thermal constant ($K = \text{slope}^{-1}$ = the number of day-degrees to complete the pre-reproductive phase), a simple regression over the linear range of the relationship between temperature (T) and developmental rates [$(R(T) = (\text{developmental time})^{-1}$] of the parasitoids was done (Campbell *et al.*, 1974).

$$R(T) = a + b * T \qquad (1)$$

A modified Logan model (Logan *et al.*, 1976) by Lactin *et al.* (1995) was used to describe the relationship between temperature and developmental rate:

$$R(T) = e^{\rho T} - e^{[\rho T_{\max} - (T_{\max} - T)/\Delta]} + \lambda \qquad (2)$$

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

Life table statistics were calculated according to Hulting *et al.* (1990) using the Jackknife program. Differences in r_m (intrinsic rate of increase) and R_o (net reproduction rate) values among populations were calculated following the protocol of Dixon (1987) and compared with Newman-Keuls tests (Sokal & Rohlf, 1995) based on jackknife estimates of variance for r_m values (Meyer *et al.*, 1986). Growth of parasitized and unparasitized larva was described by fitting the data to the equation of Sequeira & Mackauer (1992) using nonlinear least squares regression:

$$H = a/[1 + \exp(b - c*t)] \qquad (3)$$

where, H is the live mass in milligrams (mg) of parasitized and unparasitized larvae, t is days after parasitisation and a, b and c are fitted coefficients. The cumulative growth index was determined by dividing the change in growth by the time interval:

$$(H_f - H_i)*\Delta t^{-1} = G \qquad (4)$$

where, H_i is the weight of the second instar larva (prior to parasitism), H_f is the maximum weight prior to parasitoid cocoon formation and G is the cumulative growth index for the immature parasitoid stage. The relationship between days after treatment and cumulative growth index was analyzed using linear least squares regression. Spearman's correlation was used to describe the relationship between cumulative growth index and parasitoid brood and sex ratio.

All the fitted coefficients were estimated using the linear or non linear model (proc reg and proc nlr, respectively) procedure of SAS for PC (SAS Institute, 1989).

Results

Effect of host age on parasitoid survival, brood size, sex allocation and developmental time

Parasitoid-induced host mortality varied with parasitoid species ($F = 5.38$; df = 2, 69; $P = 0.0068$) and host instars ($F = 5.94$; df = 4, 69; $P = 0.0004$), but the parasitoid species × host instars interaction was not significant ($F = 1.9$; df = 8, 69; $P = 0.0743$) (fig. 1). Second instars appeared to be more affected by parasitoid-induced mortality than the other host instars (fig. 1). For all *Cotesia* species, average host mortality was >35% with second instar larvae, whereas for the 3rd–6th host instars, the highest mortality was <38%. *C. flavipes* induced host mortality in all instars, but no mortality was found in the third instar with *C. chilonis* and *C. sesamiae* (fig. 1). Percentage of hosts that produced parasitoid cocoons varied significantly among parasitoid species ($F = 7.37$; df = 2, 107; $P = 0.001$) and host instars ($F = 9.55$; df = 4, 107; $P = 0.0001$). Average % host larvae that yielded cocoons after parasitism by *C. chilonis*, *C. flavipes* and *C. sesamiae* was 47.1, 62.7 and 74.5%, respectively, using the second instar larvae as host. Thereafter, the parasitism increased and peaked at the third instar at 62.7, 74.5 and 82.4%, respectively, and subsequently decreased linearly ($Y_{Cc} = -6.3*X + 75.9$, $r^2 = 0.97$; $Y_{Cf} = -8.4*X + 86.9$, $r^2 = 0.65$; and $Y_{Cs} = -13.7*X + 111.8$, $r^2 = 0.98$; $P < 0.01$) to the sixth instar larvae.

The percentage of parasitized hosts that failed to produce cocoons but yielded host pupae varied significantly among parasitoid species ($F = 6.97$; df = 2, 107; $P = 0.0014$). For all three *Cotesia* species, the percentage of parasitized hosts that yielded host pupae increased linearly with host instar (X): $Y_{Cc} = 6.2*X + 21.6$, $r^2 = 0.94$; $Y_{Cf} = 7.1*X + 12.4$, $r^2 = 0.97$; and $Y_{Cs} = 11.2*X - 2.2$, $r^2 = 0.94$; $P < 0.001$).

The total brood size varied significantly with *Cotesia* species ($F = 39$; df = 2, 613; $P = 0.0001$) and host instars ($F = 12.8$; df = 4, 613; $P = 0.0001$) with significant interactions between parasitoid species and host instars ($F = 4.4$; df = 8, 613; $P = 0.0001$). Across all host instars, *C. sesamiae* and *C. flavipes* produced larger broods than *C. chilonis*, except with the fourth instar larvae, where there was no significant difference in brood size between *C. flavipes* and *C. chilonis* ($P > 0.05$) (fig. 2). The third instar larvae yielded the highest brood size of *C. flavipes* (80.4 ± 7.8) and *C. sesamiae* (66.7 ± 5.9).

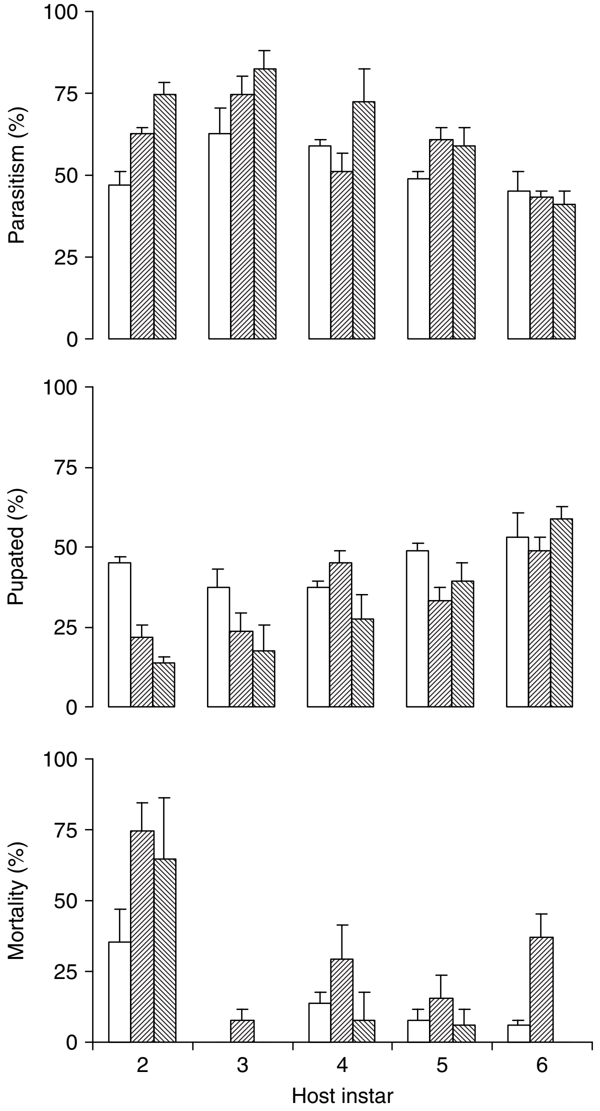

Fig. 1. Effect of *S. calamistis* instars of larvae on % parasitism, % larvae pupated and larval mortality (%). (□, *C. chilonis*; ▨, *C. flavipes*; ▧, *C. sesamiae*.)

Sex ratio of progeny varied significantly among parasitoid species ($F = 14.72$; df = 2, 604; $P = 0.0001$) and host instars ($F = 10.33$; df = 4, 604; $P = 0.0001$) with a significant interaction between parasitoid and host instars ($F = 2.26$; df = 8, 604; $P = 0.0223$). Second instar larvae parasitized by *C. chilonis* larvae yielded a significantly ($P < 0.001$) lower sex ratio than those parasitized by *C. flavipes* and *C. sesamiae* (fig. 2). *C. flavipes* had the highest sex ratio when parasitizing fourth instar larvae. For *C. sesamiae* and *C. chilonis*, the highest sex ratio was recorded with the 5th and 6th instar

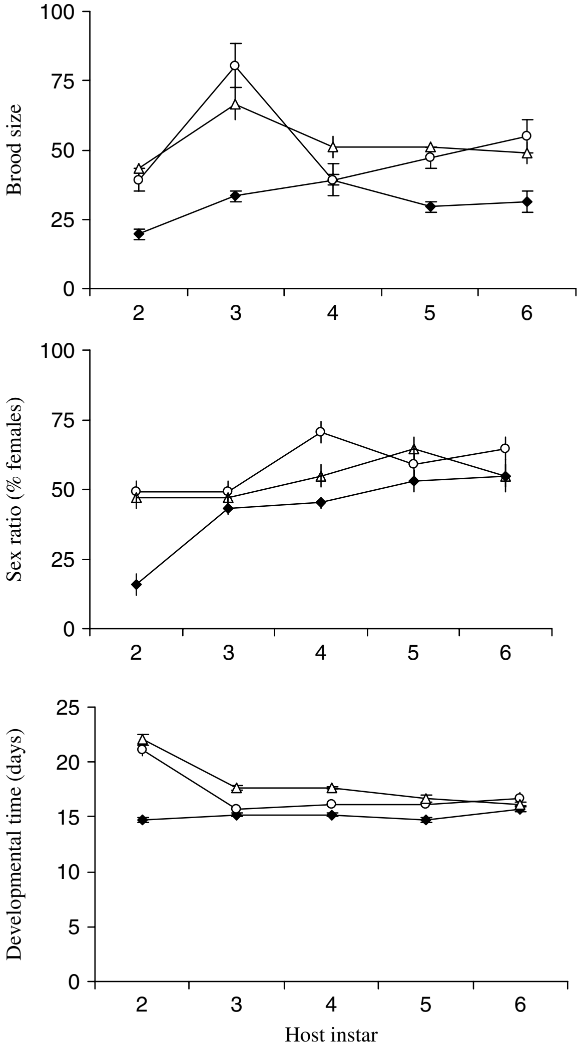

Fig. 2. Effect of *S. calamistis* instars larvae on total brood size, sex ratio and developmental time. (–◆–, *C. chilonis*; –○–, *C. flavipes*; –△–, *C. sesamiae*.)

larvae, respectively. But, there was no significant difference in sex ratio among parasitoids species with 3rd, 5th and 6th instars larvae (fig. 2).

Egg-adult developmental time of parasitoids species varied significantly among *Cotesia* species ($F = 135.8$; df = 2, 322; $P = 0.0001$) and host instars ($F = 99.3$; df = 4, 322; $P = 0.0001$). Across host age, *C. chilonis* developed faster than the other two *Cotesia* species (fig. 2). Using the second instar larvae, the developmental time of *C. chilonis* was 1.5 times faster than that of *C. flavipes* and *C. sesamiae*; while with 3rd–6th instar larvae, the difference in developmental time between *C. chilonis* and the other two *Cotesia* species was reduced by 23–28% (fig. 2).

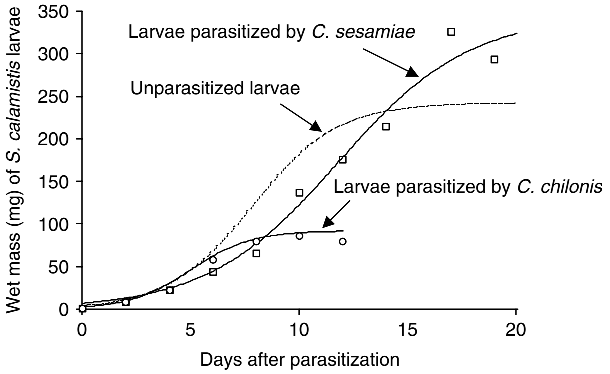

Fig. 3. Growth curve of nonparasitized *S. calamistis* larvae and parasitized larvae by *C. chilonis* and *C. sesamiae*.

Influence of parasitism on larval growth

The wet mass of live unparasitized and parasitized larvae taken at different days after parasitization was fitted to a non-linear regression. (For unparasitized larvae, $Y = 234/(1 + \exp(3.981–0.51 * t_H))$; for larvae parasitized by *C. chilonis*, $Y_{CC} = 92/(1 + \exp(3.566–0.72 * t_H))$; for larvae parasitized by *C. sesamiae*, $Y_{CS} = 345/(1 + \exp(3.883–0.33 * t_H))$; fig. 3). Comparisons of weight gain by parasitized and unparasitized larvae revealed that larvae parasitized by *C. sesamiae* reached a greater weight than unparasitized larvae ($P < 0.05$, one-tailed *t*-test); whereas, larvae parasitized by *C. chilonis* exhibited lower weight compared to the unparasitized control ($P < 0.05$, one-tailed *t*-test). This observation was consistent with the number of molts of larvae parasitized by each parasitoid; second instar larvae parasitized by *C. sesamiae* molted to the sixth instar and attained an average larval weight of 353 mg within 17 days after parasitization. Second instar larvae parasitized by *C. chilonis* only reached the fourth instar and attained a maximum weight of 107 mg within ten days after parasitization.

The cumulative growth index (Y) of larvae parasitized by *C. sesamiae* increased linearly with days after parasitization (X) ($Y_{CS} = 3.12 + 0.812 * X$, $r^2 = 0.88$, $P = 0.0002$); for *C. chilonis* $Y_{CC} = 5.40 + 0.297 * X$, $r^2 = 0.24$, $P = 0.330$.

The net weight gain by parasitized larvae was significantly positively correlated with parasitoid brood size ($r = 0.68$ and 0.89 for *C. chilonis* and *C. sesamiae*, respectively, $P < 0.02$). There was no relationship between larval weight gain and sex ratio ($r = 0.31$, $P = 0.35$ for *C. chilonis*; and $r = 0.20$, $P = 0.38$ for *C. sesamiae*).

Effect of constant temperature on the parasitism, survival and development of three Cotesia *species*

The percentage of parasitized hosts that produced parasitoid cocoons, died or pupated varied significantly ($P < 0.05$) with temperature (fig. 4). For all *Cotesia* species, % parasitized hosts that produced parasitoid cocoons were >50% at all temperatures except 32°C, and the highest rate was recorded at 28°C. At 32°C, host larvae parasitized by *C. chilonis* and *C. sesamiae* did not produce any cocoons, but <30% of host larvae produced cocoons for larvae parasitized by *C. flavipes* (fig. 4).

Between 19–30°C, larval mortality after parasitization was higher with *C. flavipes* compared to *C. chilonis* and *C. sesamiae* (fig. 4). For all parasitoids species, the highest % parasitized hosts that died was found at 32°C. Between 28–30°C, no mortality was recorded for larvae parasitized by *C. chilonis* and *C. sesamiae*.

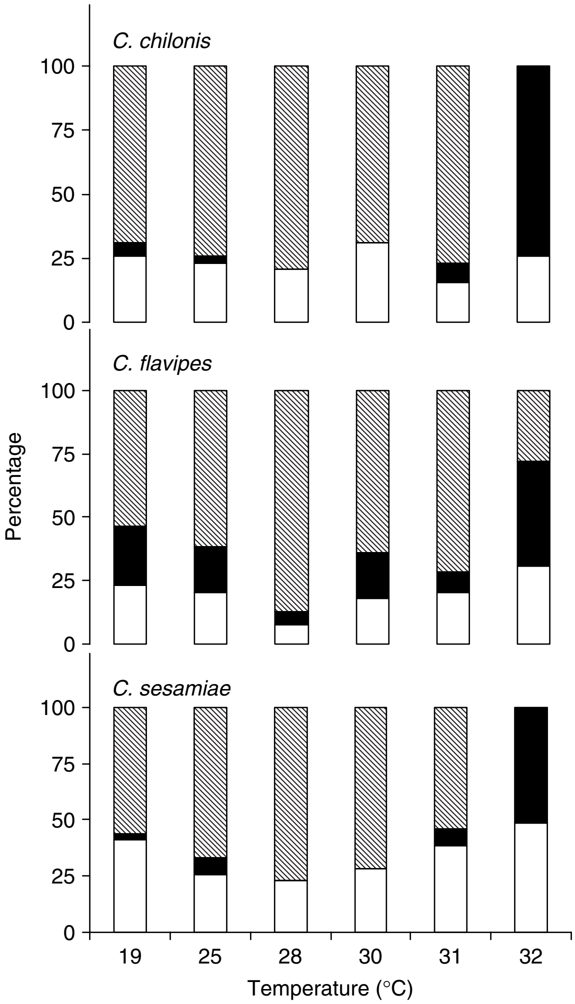

Fig. 4. Effect of constant temperature on the parasitization of *S. calamistis* larvae. (▨, % Parasitized; ■, % Died; □, % Pupated.)

For all parasitoid species, the highest % parasitized hosts that pupated was found at 32°C; pupation was higher with *C. chilonis* and *C. sesamiae* than with *C. flavipes* between 19–30°C.

There were no significant differences ($P > 0.05$) in developmental time of male and female parasitoids, thus data gathered on developmental time were pooled across sexes for further analyses. Egg-adult developmental time decreased significantly (table 2) as temperature increased (between 19–30°C for *C. chilonis* and *C. sesamiae* and 19–31°C for *C. flavipes*). Only *C. flavipes* completed development at 32°C (table 2).

Effect of constant temperature on the developmental rate of three Cotesia *species*

Developmental rates increased linearly between 19–30°C for *C. chilonis* and *C. sesamiae* and between 19–31°C for *C. flavipes* (fig. 5). The lower developmental threshold calculated from the linear regression of temperature (T) on developmental rate was 14.3, 13.8 and 13.8°C for *C. chilonis*, *C. sesamiae* and *C. flavipes*, respectively; and the thermal requirement for completion of the pre-reproductive phase was 212.8, 238.1 and 222.2 degree-days above the lower developmental threshold.

The modified Logan model gave a good fit to the data sets for all parasitoid species within the lower and upper threshold ($r^2 > 0.94$, $P < 0.0001$; fig. 5, table 3). The fitted parameters of the model were estimated and presented in table 3. The lower developmental threshold estimated from the non-linear regression of temperature (T) on developmental rate was 15.9, 15.9 and 14.9°C for *C. chilonis*, *C. sesamiae* and *C. flavipes*, respectively; and the upper lethal temperature was 34.2, 35.2 and 33.8°C for *C. chilonis*, *C. sesamiae* and *C. flavipes*, respectively.

Effect of constant temperature on the reproductive potentials of three Cotesia *species, using* S. calamistis *as host*

There was no significant ($P > 0.05$) difference in the number of larvae attacked among *Cotesia* species. A

Table 2. Effect of constant temperature on the emergence and egg-adult developmental time (mean ± SE) of three *Cotesia* species.

Variables	Temperature (°C)	Species *C. chilonis*	*C. flavipes*	*C. sesamiae*
Emergence (%)	19	86.4 ± 2.3aA	74.5 ± 10.1aA	81.8 ± 6.0aA
	25	94.1 ± 1.4aA	78.9 ± 3.7aA	96.2 ± 1.2aA
	28	91.6 ± 1.9aA	86.1 ± 2.0aA	94.8 ± 1.3aA
	30	51.1 ± 3.6bB	85.6 ± 3.1aA	74.8 ± 2.4aA
	31	4.1 ± 1.0cC	83.6 ± 2.5aA	62.6 ± 4.8bB
	32	–	26.3 ± 5.1b	–
Developmental time (days)	19	49.4 ± 0.2aB	54.3 ± 1.8aA	53.1 ± 0.4aA
	25	18.4 ± 0.1bB	20.2 ± 0.3bA	19.9 ± 0.1bA
	28	15.1 ± 0.1dB	16.1 ± 0.1cdA	16.1 ± 0.1cA
	30	14.4 ± 0.1eC	15.0 ± 0.2cdB	15.7 ± 0.1cA
	31	15.7 ± 0.1cA	14.2 ± 0.1cB	16.0 ± 0.1cA
	32	–	17.0 ± 0.2d	–

Within a column, means followed by different lower case letters are significantly different (comparison between temperatures). Within a row, means followed by different capital letters are significantly different (comparison between species), $P \leqslant 0.05$ (*t*-test).

maximum of four ovipositions were observed per female during her entire life span ranging from 1.3 days for *C. chilonis* and *C. flavipes* to 1.6 days for *C. sesamiae*. The highest number of adult progeny was recorded at 28°C for *C. chilonis* and *C. flavipes*, while the numbers of offspring for *C. sesamiae* were the same at all temperatures tested (table 4).

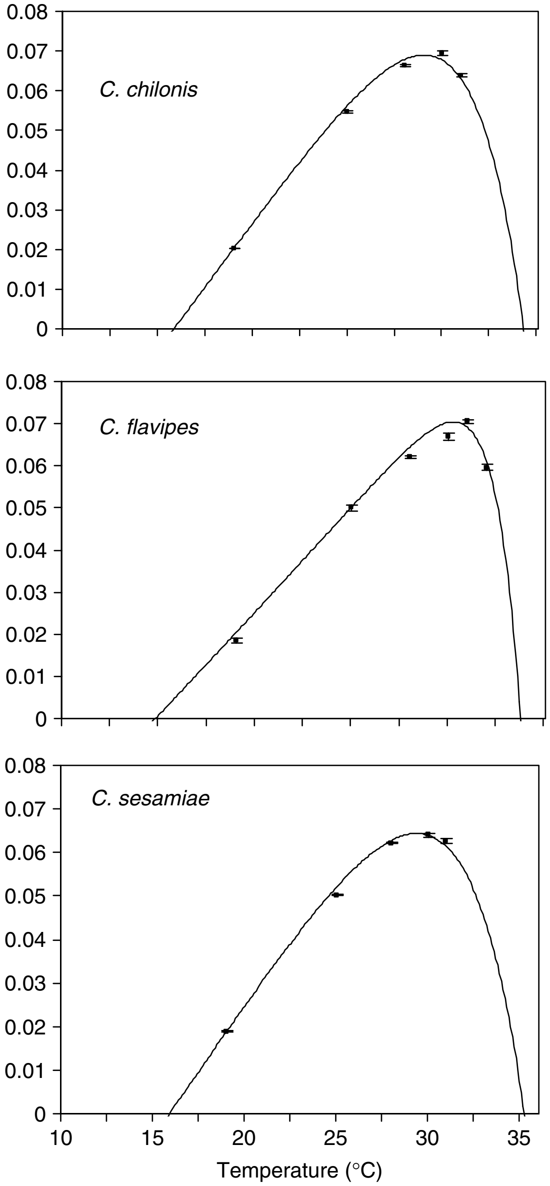

Fig. 5. Effect of temperature on the developmental rate of *C. chilonis*, *C. flavipes* and *C. sesamiae*, using *S. calamistis* as host.

Across temperatures, *C. flavipes* yielded the highest offspring, following by *C. sesamiae* and *C. chilonis*. The sex ratios did not vary significantly with species and temperature (table 4). Across temperatures, the first brood of *C. chilonis*, *C. flavipes* and *C. sesamiae* accounted for, respectively, 66.6 ± 4.0, 67.7 ± 3.9, 50.9 ± 3.5% of the total; and the sex ratio was, respectively, 41.7 ± 3.3, 60.4 ± 3.2 and 66.4 ± 3.7% for *C. chilonis*, *C. flavipes* and *C. sesamiae*.

The life table parameters varied significantly with temperatures and among parasitoids species (table 5). The intrinsic rate of increase (r_m) and net reproductive rate (R_o) increased significantly with temperature and peaked at 28°C. Mean generation time and doubling time decreased linearly between 19–30°C.

Discussion

Host size has long been recognized as a major attribute of host quality (Salt, 1940). Because large hosts contain more resources, they are considered to be of higher quality than small ones (Charnov *et al.*, 1981; Charnov, 1982; King, 1987). In the present study, the three *Cotesia* species attacked and successfully completed development in all larval stages of *S. calamistis* except for first instars. However, second instars suffered more from parasitoid-induced mortality than 3rd–5th instars. Similarly, Jiang *et al.* (2004) found that parasitoid-induced mortality was higher in third than the fourth larval instar of *C. partellus* when the host larva was attacked by *C. flavipes*. In the present study, the proportion of instars that pupated after being parasitized increased linearly with host age at parasitization, indicating encapsulation of parasitoid progeny by the host immune system when older host instars were attacked. According to van Alphen & Drijver (1982), in younger larvae, the risk of encapsulation is lower because their immune system is not as advanced as that of older larvae. Thus, the high larval mortality, following attack by parasitoid females, observed in second instar hosts is probably due to oviposition associated trauma or from complications that arise subsequent to physiological interaction between the host and the parasitoid (Vinson & lwantsch, 1980; Boultreau, 1986). For example, Harvey *et al.* (1994) showed that, when the koinobiont ichneumonid larval parasitoid *Venturia canescens* (Gravenhorst) attacked second instars of the pyralid *Plodia interpunctella* Hübner, up to 50% of the larvae died, which was attributed to mutilation of the larval host with insertion and removal of the ovipositor during parasitism. Furthermore, Kajita & Drake (1969) and Ngi-Song *et al.* (1995) reported that host mortality from the act of parasitism was greater when young larval instars were attacked. When assessing the impact of a natural enemy, field parasitism, usually calculated as the percentage of suitable life stages yielding parasitoids, is the most widely used parameter. *C. flavipes* was released in coastal Kenya for control of the invasive *C. partellus* in 1993. Borer densities started to decline

Table 3. Fitted coefficients of a modified Logan model (Logan *et al.*, 1976) by Lactin *et al.* (1995).

Species	ρ	T_{max}	Δ	λ	r^2	*P*-value
C. chilonis	0.0059	40.9196	2.8633	−1.0977	0.989	< 0.0001
C. flavipes	0.0045	37.0716	1.3278	−1.0693	0.945	< 0.0001
C. sesamiae	0.0057	43.2067	3.4447	−1.0938	0.989	< 0.0001

Table 4. Effect of constant temperature on the total progeny and sex ratio (mean ± SE) of three *Cotesia* species.

Variables	Temperature (°C)	Species		
		C. chilonis	*C. flavipes*	*C. sesamiae*
Total progeny	19	14.7 ± 1.5 bC	29.2 ± 7.1 cB	47.5 ± 5.9 aA
	25	38.2 ± 3.2 aB	48.6 ± 7.2 bA	58.6 ± 6.4 aA
	28	40.4 ± 3.3 aC	91.8 ± 9.1 aA	58.0 ± 4.6 aB
	30	20.2 ± 1.7 bB	58.4 ± 8.3 bA	51.4 ± 2.8 aA
Sex-ratio (% females)	19	67.7 ± 7.5	58.5 ± 5.6	47.9 ± 6.5
	25	51.6 ± 4.1	74.3 ± 3.4	55.0 ± 5.5
	28	51.6 ± 3.8	66.0 ± 5.3	65.2 ± 5.2
	30	55.2 ± 4.6	70.8 ± 6.2	61.0 ± 7.4

Within a column, means followed by different lower case letters are significantly different (comparison between temperatures); within row, means followed by different capital letters are significantly different (comparison between species), $P \leqslant 0.05$ (*t*-test).

Table 5. Effect of temperature on average (± SE) of life table parameters of three *Cotesia* species.

Parameter/species	Temperature (°C)			
	19	25	28	30
r_m				
C. chilonis	0.050 ± 0.002dB	0.160 ± 0.004bB	0.209 ± 0.006aB	0.106 ± 0.006cC
C. flavipes	0.054 ± 0.005dAB	0.105 ± 0.008cC	0.215 ± 0.007aB	0.162 ± 0.010bB
C. sesamiae	0.063 ± 0.002dA	0.189 ± 0.006cA	0.268 ± 0.005aA	0.222 ± 0.004bA
R_0				
C. chilonis	11.15 ± 1.121bB	19.24 ± 1.528aB	20.67 ± 1.686aC	11.12 ± 0.966bB
C. flavipes	15.45 ± 3.755cAB	35.99 ± 5.309bA	60.60 ± 6.018aA	40.99 ± 5.790bA
C. sesamiae	22.72 ± 2.848bA	32.26 ± 3.495aA	37.76 ± 2.973aB	31.40 ± 1.735aA
G				
C. chilonis	48.6	18.5	14.5	14.5
C. flavipes	50.6	19.5	15.5	14.5
C. sesamiae	50.6	19.5	16.5	15.5
DT				
C. chilonis	14.0	4.3	3.3	6.5
C. flavipes	12.8	6.6	3.2	4.3
C. sesamiae	11.2	3.7	2.6	3.1
λ				
C. chilonis	1.05	1.17	1.23	1.18
C. flavipes	1.06	1.20	1.30	1.29
C. sesamiae	1.06	1.19	1.25	1.25

Within a row, means followed by different lower case letters are significantly different (comparison between temperatures); within column, means followed by different capital letters are significantly different (comparison between species), $P \leqslant 0.05$ (Student-Newman-Keul test); r_m, intrinsic rate of natural increase; R_0, net reproductive rate; G, mean generation time (days); DT, doubling time (days); λ, finite rate of increase.

rapidly at parasitization rates of less than 10%, and they never exceeded 30% (Jiang *et al*., 2006). By 2004, pest densities were reduced by 75%. These low parasitism rates cannot explain the impact the parasitoid had on pest populations. However, in view of the high mortality occurring in younger larval instars when attacked by *Cotesia* spp. found in the present study, basing the success of a parasitoid on parasitism of suitable life stages only would highly underestimate the possible impact a parasitoid can have in the field. Young *C. partellus* larvae move to the whorl where they either feed on the leaves or disperse to other plants (Päts & Ekbom, 1992). Thus, it is hypothesized that in the field, *C. flavipes* is frequently attacking exposed young larval instars, most of which die or probably drop from the plant. As a result, the cumulative mortality of *C. partellus* is higher than estimated from successful parasitism alone.

In the present study, larvae parasitized by *C. chilonis* exhibited a reduced growth trajectory compared to unparasitized larvae. This was also reported by Sequeira & Mackauer (1992) for the pea aphid parasitized by *Aphidius ervi* Halyday. This apparent inability to regulate continued host growth was not evident for larvae parasitized by *C. sesamiae*. Second instar larvae parasitized by *C. sesamiae* first continued to grow at the same rate and then surpassed growth of unparasitized larvae, suggesting that the immature parasitoid remained quiescent until the host attained a suitable size before it commenced its destructive attack on the tissue. Polydnaviruses (PDVs) are known to cause developmental arrest in hosts parasitized by braconid parasitoids (Beckage *et al*., 1994; Beckage & Gelman, 2004). Recent studies revealed two types of PDV in *C. sesamiae* in Kenya, one associated with the coastal and one with the inland strain of the parasitoid (Gitau, 2006). The differences in the growth trajectory of *S. calamistis* caused by the two *Cotesia* species might have been due to differences in the functional role of PDVs.

In gregarious species, parasitoid fitness is not only affected by host size but also by the number of parasitoid developing in the host (Waage & Godfray, 1985; Charnov & Skinner, 1988; Alleyne & Beckage, 1997). Our findings showed that the net weight gain by parasitized larvae was significantly positively correlated with parasitoid brood size in all the three parasitoids species. However, the second instar host larvae yielded significantly fewer female offspring of *C. chilonis* compared to *C. flavipes* and *C. sesamiae*. Similarly, Wellings *et al*. (1986) found that the braconid koinobiont *A. ervi* produced a male-biased sex ratio in smaller hosts. They hypothesed that differential mortality, rather than facultative control of sex ratio, was the main cause of a male-biased sex ratio in smaller hosts, with female offspring less likely to survive in smaller hosts. According to Charnov *et al*. (1981) and Godfray (1994), the production of male broods in less fit hosts is an evolutionally adaptation; if small hosts are the result of low plant vigor caused by, for example, low soil fertility or adverse climatic conditions (Schulthess *et al*., 1997b), a female biased sex ratio in small hosts may cause local extinction of both the host and parasitoid. The higher parasitism rates by *C. sesamiae* compared to *C. chilonis* may also be a result of a higher acceptance of the host by the former. If this is the case, differences in sex ratio may, indeed, be the results of facultative control of the sex ratio, whereby the parasitoids refuses to oviposit or decides to oviposit mainly unfertilized eggs.

The developmental threshold of *C. flavipes* was lower than that of *C. chilonis* and *C. sesamiae*. However, the percent of adults emerged between 19–30°C was similar in all three *Cotesia* species. If temperature was the main driving factor determining the performance of a parasitoid, *C. flavipes* would have a higher ability to adapt to a new area than the other two species. In fact, in Kenya, after its release in 1993, *C. flavipes* is now recovered from 0 to 2000 m above sea level (Eric Muchugu, ICIPE, Nairobi, Kenya, unpublished data).

The optimal and maximum temperatures obtained from the nonlinear model were very high. However, the thermal constants of the three *Cotesia* species were considerably (>3 times) shorter than the 761 day-degrees obtained for its host *S. calamistis* (Shanower *et al*., 1993). Furthermore, the r_m of *S. calamistis* reported by Sétamou *et al*. (1993) were 50–96% at 25°C and 74–97% at 28°C (depending on nitrogen content in stems) of the values calculated for the three *Cotesia* species. Thus, in terms of thermal requirements and biotic potential, the three *Cotesia* species are considerably superior to their host *S. calamistis*. In addition, differences in r_m between parasitoid species indicate that *C. sesamiae* will out-compete both *C. flavipes* and *C. chilonis* over the temperature range of 19–30°C with *S. calamistis* as host. On the other hand, the inability of *C. chilonis* to regulate continued growth of the parasitized host, coupled with the production of male-biased broods, makes the parasitoid inferior to the other two species, as also indicated by the lowest r_m.

All three *Cotesia* spp. were released in Benin but only *C. sesamiae* finally established. Based on the results of the present study alone, this could not have been predicted although, in terms of biotic potential only, it was superior to the other two *Cotesia* species. However, the other main borer species in the region, the pyralid *Eldana saccharina* Walker, which is unsuitable to all three species (Hailemichael, 1998), was accepted for oviposition by both *C. flavipes* and *C. chilonis* and, thus, may have acted as a reproductive sink. Consequently, only *C. sesamiae* is being considered for releases in western Africa. A Kenyan inland strain of *C. sesamiae* will be released against *B. fusca* in the humid forest zone and the Western Highlands in Cameroon. The present findings suggest that temperature will not be a limiting factor and that the parasitoid will establish in both ecozones.

The present study investigated the physiological suitability of *S. calamistis* for the three *Cotesia* spp., while other studies have examined suitability of other West African stemborers. However, the success of a parasitoid depends, not only on physiological compatibility with its host, but also on the suitability of other acceptable hosts occurring in the system and its ability to find hosts and intrinsic competition within hosts. Additionally, host finding and competition studies may help to better understand the establishment and dynamics of these parasitoids once released in nature.

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