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Temperature influence on cohort parameters and demographic characteristics of the two cowpea coreids *Clavigralla tomentosicollis* and *C. shadabi*

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Abstract

Age-specific life tables of two important pests of cowpea, *Vigna unguiculata* (L.) Walp., the pod sucking bugs *Clavigralla tomentosicollis* Stål and *C. shadabi* Dolling (Heteroptera: Coreidae), were obtained from observations carried out at different temperatures. A biophysical model was found satisfactory to describe the temperature-response of developmental and mortality rates of egg and nymphal stages, with a peak developmental rate around 34 °C in both species. The variability in development times was small and the experimental data did not permit any conclusion with regard to the Erlang probability density function. Survival of eggs and nymphs remained high between 20 ° and 30 °C for both species. At temperatures above 34 °C, *C. tomentosicollis* survivorship and fecundity was higher than that of *C. shadabi*, which in turn laid more eggs at temperatures between 20 ° and 30 °C. Maximum fecundity is estimated to be at 29 °C for *C. tomentosicollis* (99 eggs/female) and 26 °C for *C. shadabi* (261 eggs/female). At 30 °C, the intrinsic rate of increase reached a maximum in both species, 0.152 per day for *C. tomentosicollis* and 0.145 per day for *C. shadabi*, and remained high for *C. tomentosicollis* until 36 °C. *C. tomentosicollis* performed significantly better on pigeonpea, *Cajanus cajan* Millsp., than on cowpea at higher temperatures.

Introduction

Cowpea, *Vigna unguiculata* (L.) Walp., is attacked by numerous insect pests throughout its growth cycle. Heavy crop losses due to insect damage are reported for many cowpea production areas (e.g., Singh *et al.*, 1990). In Africa, a species complex of heteropteran pod sucking bugs (PSB) can cause high levels of seed damage in most areas where cowpea is grown for grain (Jackai & Daoust, 1986). In southern Benin, the PSB are considered to be the most damaging post-flowering pest group, causing up to 80% of seed damage (Dreyer *et al.*, 1994). Among the PSB, mainly two species, the coreids *Clavigralla tomentosicollis* Stål and *C. shadabi* Dolling, were observed reproducing readily in the field. Population development is driven primarily by the number of adults immigrating into the cowpea field, their reproduction rate, and mortality of offspring that may ensue. Many biotic and abiotic factors act on the population. Ambient temperature, nutrition and natural enemies are among the most important factors governing population increase. In the present study, consideration was given to temperature since it is the main environmental factor controlling the poikilothermic development of insects (Wigglesworth, 1972).

Several studies provide information on the developmental biology of both species on different food plants (Materu, 1968; Egwuatu & Taylor, 1977a,b; Jackai & Inang, 1992), but they were either carried out under uncontrolled temperature conditions or focussed on development and mortality without considering fecundity.

C. tomentosicollis breeds and develops on pigeonpea, *Cajanus cajan* Millsp., throughout the year (Egwuatu & Taylor, 1977c, 1983). In West Africa, pigeonpea is usually grown as a backyard or hedge crop and often occurs in the same area where cowpea is cultivated. It is therefore an important potential breeding site. Both pigeonpea and cowpea play an important part in the seasonal biology of *C. tomentosicollis* (Egwuatu & Taylor, 1977b). For this reason, and because pigeonpea will be tested as a trap plant for *C. tomentosicollis* in a subsequent study, the insect was also tested on pigeonpea.

The purpose of the present study was to evaluate the effect of temperature on cohort development and fecundity of *C. tomentosicollis* and *C. shadabi*. Since this study will be used to construct an explicative model on cohort and population dynamics the relevant temperature-dependent relationships will be based on a deep level of understanding. Thereby, known demographic techniques will be applied. The information obtained is used to compare the population growth potential of *C. tomentosicollis* on its two most important, West African host plants, and to assess the performance of the two species on cowpea.

Materials and methods

Development, mortality, fecundity and longevity of both species were experimentally determined under standard conditions, by excluding natural enemies and providing optimal food supplies at different temperatures. The experiments with *C. tomentosicollis* were done on cowpea and pigeonpea, and with *C. shadabi* on cowpea only.

Experimental set-up

Adults of *C. tomentosicollis* and *C. shadabi* were collected from cowpea planted at the IITA Station in Abomey/Calavi, Benin. They were fed with fresh green pods of a local cowpea variety ('Kpodjiguégué'), taken from plants grown in the greenhouse on 'cowpea towers', a modification of the 'cassava trees' as reported by Neuenschwander & Haug (1992).

For the experiment with *C. tomentosicollis* on pigeonpea, adult females were obtained from infested plants of a local pigeonpea cultivar in the neighbourhood of IITA Station.

For the experiment with *C. tomentosicollis* on cowpea, eight constant temperatures (± 1 °C) were used: 15°, 18°, 20°, 23°, 25°, 30°, 34° and 36 °C. On pigeonpea, the insects were kept at 18°, 20°, 23°, 25°, 28°, 30°, 34° and 36 °C. *C. shadabi* was exposed to temperatures of 15°, 18°, 20°, 23°, 25°, 28°, 30°, 34° and 36 °C. Percival® (Percival Manufacturing Co., Boone, Iowa 50036, U.S.A.) incubators were used for the experiments. The photoperiod was kept at L12:D12 and relative humidities between 70 and 90%. A minimum of 100 eggs from each species (Tables 1 and 2), less than 24 h old, were exposed to each of the temperatures, and checked every 24 h for hatching.

After eclosion, the first-instar nymphs were reared individually in plastic Petri dishes (80 mm diameter × 10 mm high) with a 2 cm-piece of fresh cowpea pod less than 10 days old. Pod pieces were changed daily to prevent drying up. For *C. tomentosicollis* on pigeonpea, whole pods were supplied. Percentage adult emergence and sex of the individuals were recorded.

To determine oviposition capacity and longevity, freshly emerged females were kept in pairs in Petri dishes at each of the temperatures indicated above. Thirty pairs were used for each temperature, except 18 °C for which 20 pairs were used. Cowpea pods were cut into 4 cm-long pieces and one piece offered as food to each pair of bugs. Eggs were counted daily and removed and female survivorship was recorded. Dead males were replaced.

Analysis of temperature influence on cohort parameters

Development time. The observed development time, $D(T_c)$, of both the egg stage and the nymph stage was expressed as

$$D(T_c) = \frac{1}{r(T_c)} \qquad (1)$$

where $r(T_c)$ is the development rate per day at constant temperature T_c.

The rates can be related to temperature using different nonlinear models. A critical evaluation of several models is given by Lamb *et al.* (1984). Wagner *et al.* (1984) reviewed the literature on the same topic with particular reference to a biophysical approach and its application. In this study, preference was given to a biophysical model, originally formulated by Sharpe & DeMichele (1977) and modified by Schoolfield *et al.* (1981). The level of understanding of the model is based on enzyme kinetics and assumes that speed of development is driven by a single rate-controlling enzyme. Accordingly, the relationship between the developmental rate, $r(T_c)$, and the absolute temper-

Table 1. *C. tomentosicollis* cohort development and survivorship of pre-imaginal instars on cowpea pods under controlled conditions. T: constant temperatures in environmental cabinets, Nb: initial cohort number, Ne: number of surviving individuals, $D(T_c)$: mean duration [in days] of an instar at temperature T and associated variance s^2, N1–N5: first–fifth nymphal instar

Instar	T [°C]	Nb	Ne	Survival	$D(T_c)$	s^2
egg	18	315	156	0.495	16.67	5.763
	20	144	122	0.847	9.35	0.452
	23	740	717	0.969	8.00	0
	25	104	99	0.952	7.35	0.653
	30	118	102	0.864	4.98	0.029
	34	629	530	0.843	3.00	0
	36	106	88	0.830	3.31	0.216
N1	18	155	80	0.516	4.48	0.380
	20	100	88	0.880	2.72	0.459
	23	100	99	0.990	2.18	0.212
	25	99	78	0.788	2.14	0.123
	30	100	91	0.910	2.03	0.027
	34	100	74	0.740	1.42	0.247
	36	100	94	0.940	1.55	0.250
N2	18	80	67	0.838	6.49	2.162
	20	88	86	0.977	4.98	0.999
	23	99	92	0.929	4.39	1.095
	25	78	73	0.936	3.21	0.360
	30	91	89	0.978	1.77	0.522
	34	74	65	0.878	1.41	0.247
	36	94	86	0.915	1.24	0.234
N3	18	67	64	0.955	6.33	0.541
	20	86	86	1	4.61	0.854
	23	92	88	0.957	3.37	0.556
	25	73	69	0.945	3	0.358
	30	89	89	1	1.65	0.250
	34	65	53	0.815	1.28	0.207
	36	86	85	0.988	1.45	0.250
N4	18	64	60	0.938	7.25	0.936
	20	86	81	0.942	5.10	0.750
	23	88	84	0.955	4.20	0.332
	25	69	66	0.957	3.16	0.487
	30	89	88	0.988	0.98	0.123
	34	53	47	0.887	1.49	0.342
	36	85	80	0.941	1.57	0.273
N5	18	60	52	0.867	12.50	0.759
	20	81	54	0.667	7.94	1.610
	23	84	82	0.976	6.62	0.492
	25	66	59	0.894	5.46	0.288
	30	88	83	0.943	3.31	0.257
	34	47	44	0.936	2.57	0.391
	36	80	60	0.750	2.30	0.214

Table 2. *C. shadabi* cohort development and survivorship of pre-imaginal instars on cowpea pods under controlled conditions. T: constant temperatures in environmental cabinets, Nb: initial cohort number, Ne: number of surviving individuals, $D(T_c)$: mean duration [in days] of an instar at temperature T and associated variance s^2, N1–N5: first–fifth nymphal instar

Instar	T [°C]	Nb	Ne	Survival	$D(T_c)$	s^2
egg	18	163	103	0.632	21.28	2.340
	20	100	80	0.800	12.99	3.480
	23	170	123	0.724	9.52	0.249
	25	181	125	0.940	7.69	0.223
	28	160	151	0.944	6	0
	30	100	93	0.930	5	0
	32	360	208	0.578	4.95	0.230
	34	372	168	0.452	4.26	0.307
N1	18	98	10	0.102	9.09	4.322
	20	117	94	0.803	5.05	1.073
	23	100	93	0.930	3.52	1.905
	25	125	111	0.888	2.87	0.754
	28	100	94	0.940	3.14	0.128
	30	100	94	0.940	2.04	0.063
	32	100	67	0.670	1.57	0.310
	34	120	33	0.275	1.39	0.371
N2	18	10	3	0.300	10.64	1.333
	20	94	77	0.819	8	1.733
	23	93	71	0.763	3.88	0.618
	25	111	101	0.910	3.70	0.467
	28	94	71	0.755	3.16	0.285
	30	94	86	0.915	3.15	0.247
	32	67	51	0.761	2.38	0.478
	34	33	23	0.697	2.39	0.249
N3	18	3	3	1	8	1
	20	77	72	0.935	6.85	0.572
	23	71	67	0.944	3.62	0.571
	25	101	100	0.990	3.06	0.219
	28	71	71	1	2.87	0.284
	30	86	85	0.988	2.44	0.298
	32	51	46	0.902	2.22	0.307
	34	23	22	0.957	2.18	0.346
N4	18	3	3	1	7.69	0.333
	20	72	70	0.972	7.46	0.369
	23	67	65	0.970	3.88	0.672
	25	100	100	1	3.60	0.283
	28	71	70	0.986	2.99	0.217
	30	85	85	1	2.81	0.274
	32	46	46	1	2.37	0.283
	34	22	21	0.950	2.28	0.214
N5	18	3	3	1	12.66	0.333
	20	70	68	0.970	12.05	0.724
	23	65	63	0.969	6.80	1.608
	25	100	100	1	5.75	0.285
	28	70	69	0.986	5.08	0.845
	30	85	85	1	4.48	0.324
	32	46	44	0.957	3.64	0.562
	34	21	18	0.857	3.23	0.183

ature, T_c [°K], is expressed as

$$r(T_c) = \frac{\rho \frac{T}{298.16} \exp\left[\frac{\Delta H_A^{\#}}{R}\left(\frac{1}{298.16} - \frac{1}{T}\right)\right]}{1 + \exp\left[\frac{\Delta H_L}{R}\left(\frac{1}{T_{1/2_L}} - \frac{1}{T}\right)\right] + \exp\left[\frac{\Delta H_H}{R}\left(\frac{1}{T_{1/2_H}} - \frac{1}{T}\right)\right]} \quad (2)$$

where

ρ = development rate [per day] at 25 °C [T = 298.16 °K], assuming no enzyme inactiviation,

$\Delta H_A^{\#}$ = enthalpy of activation of the reaction that is catalyzed by the enzyme [cal mol^{-1}],

R = universal gas constant [1.987 cal °K^{-1} mol^{-1}],

ΔH_L = change in enthalpy associated with low temperature inactivation of the enzyme [cal mol^{-1}],

$T_{1/2_L}$ = temperature [°K] at which the enzyme is 1/2 active and 1/2 low temperature inactive,

ΔH_H = change in enthalpy associated with high temperature inactivation of the enzyme [cal mol^{-1}],

$T_{1/2_H}$ = temperature [°K] at which the enzyme is 1/2 active and 1/2 high temperature inactive.

The values of the six unknown parameters in equation [2] were estimated by least square regression. The dependent variable is the daily development rate, $r(T_c)$, which was determined at the different constant temperatures indicated above. According to Jackai & Inang (1992) the thermal death point of *C. tomentosicollis* is reached at 40 °C, accordingly $r(T_c)$ was set equal to zero at this temperature and included in the analysis.

The model has great explanatory capabilities (Wagner *et al.*, 1984) and has been applied successfully to several insect species (e.g., Hilbert & Logan, 1983; Cerutti, 1989; Roux, 1993). It is particularly suitable for insects that are exposed in nature to temperatures beyond the range in which a linear rate-temperature model is applicable (Campbell *et al.*, 1984).

Mortality. Overall mortality is the compound measure of external and innate mortality (Curry & Feldman, 1987). Innate mortality, the subject of this study, is a function of age and temperature for all poikilotherms. Following Curry & Feldman (1987), data on temperature-dependent survivorship, $\varepsilon(T_c)$, for eggs and the five nymphal instars lumped together were fitted to equation [2]. Thus, mortality is expressed on the level of enzyme kinetics and parameters ρ, $\Delta H_A^{\#}$, R, ΔH_L, $T_{1/2_L}$, ΔH_H and $T_{1/2_H}$ were replaced by $p_1 \ldots p_6$, respectively (see Table 3).

Variability in development times. Since genetic differences among individuals result in variable developmental rates, individuals in the same constant temperature emerge at different times. To select a model that accounts for the stochastic properties of the development process, the approach proposed by Severini *et al.* (1990) is followed. Accordingly, the development process was represented using a series of H substages. In following the development through a life stage is considered to be conservative, that is, without mortality. Accordingly, the basic equation describing the frequency distribution of emergence times, $r_H(t)$, is known as the Erlang Probability Density Function:

$$r_H(t) = \frac{c^H}{(H-1)!} \exp^{-ct} t^{H-1} \quad (3)$$

H represents the number of substages, that is, the degree of stochasticity of the developmental process, and is called the 'shape parameter' since it determines the shape of the density function (Manetsch, 1976; Vansickle, 1977; Severini *et al.*, 1990). The constant c is called the 'scale parameter'.

In the temperature range with limited innate mortality, conservative development occurs and H is assumed to be constant. Observed pooled frequencies of individual transit times of nymphs from cohorts kept at different temperatures were used to determine $D(T_c)$ and the corresponding variance $s^2(T_c)$. The development times of eggs were not included in the analysis, because the experimental conditions (daily observations) did not permit an assessment of the apparently small variability in development times. Equation [3] was fitted to the normalized observed transit times, t, of both species using the software package 'STATGRAPHICS'. The parameter H representing their variabilities was determined accordingly.

Longevity and fecundity. For each temperature, the senescence rate $z(T_c)$, i.e., the inverse of the average life span, was calculated for all *C. tomentosicollis* and *C. shadabi* females. Note that air temperature and not insect body temperature is represented. It is assumed that $z(T_c)$ is proportional to temperature between the lower thermal threshold and 35 °C. At temperatures exceeding 35 °C the senescence rate is assumed to

Table 3. Parameter values for the biophysical model [eq. 2] describing temperature influence on stage-specific pre-imaginal development and survivorship and on the intrinsic rate of increase (r_m) of the two pod sucking bugs *C. tomentosicollis* and *C. shadabi* (temperature is given in Kelvin degrees: 273.16° K = 0° C). Parameters p1–p6 correspond to survival and r_m (see text)

Process	*Clavigralla* species	Stage	Model parameters						R^2
			ρ	$\Delta H_A^{\#}$	ΔH_L	$T_{1/2_L}$	ΔH_H	$T_{1/2_H}$	
development	*tomentosicollis*	eggs	0.143	15682	–1759810	291.0	1560988	309.3	0.989
		nymphs	0.059	14415	–1415451	291.0	335497	310.1	0.998
	shadabi	eggs	0.147	8932	–59507	291.5	2392173	309.0	0.993
		nymphs	0.050	10000	–170000	292.0	6000000	308.0	0.989
			p1	p2	p3	p4	p5	p6	
survival	*tomentosicollis*	eggs	0.953	–3101	–149126	291.3	1972596	311.8	0.998
		nymphs	0.620	0	–946250	291.1	92659000	311.0	0.720
	shadabi	eggs	0.867	6176	–1204952	290.7	101738	305.7	0.900
		nymphs	0.756	–950	–2345190	291.4	220419	305.7	0.962
r_m	*tomentosicollis* (on cowpea)		0.171	–4874	–74642	297.6	1934341	311.8	0.916
	tomentosicollis (on pigeonpea)		0.047	63066	–105399	304.4	353987	308.5	0.997
	shadabi		0.099	11480	–164898	294.0	1955048	305.1	0.975

be constant. Accordingly, the data were subjected to linear regression analysis.

To describe the fecundity response to temperature, $g(T_c)$, the following second-order polynomial regression model was used:

$$0 \leq g(T_c) = a + bT_c + cT_c^2 \tag{4}$$

where a, b and c are coefficients estimated by least square regression.

To illustrate the distribution of eggs laid over the female's life span, the age-specific fecundity rate, $f(a)$, was calculated for the cohort kept at 30 °C. The data were fitted to the following empirical model (Bieri *et al.*, 1983; Bianchi *et al.*, 1990):

$$0 \leq f(a) = \frac{c_1 \cdot (a - c_2)}{c_3^{(a-c_2)}} \tag{5}$$

where a is the age in days of the female and parameters $c_{1\ldots3}$ are estimated by least square procedures.

Analysis of temperature influence on demographic characteristics

The intrinsic (instantaneous) rate of increase, r_m, is useful in comparing the comprehensive effects of fecundity, speed of development and mortality (Andrewartha & Birch, 1954; Krebs, 1985). Survival and reproduction were examined using a life table analysis according to Hulting *et al.* (1990), whose programme provides a 'Jackknife' estimate of r_m with its standard error (SE). The standard error is obtained by the jackknife technique described in detail elsewhere (see Krebs, 1989, pp. 464–465). r_m is calculated from the following equation derived by Lotka (1907):

$$\sum_0^\infty e^{-r_m \cdot x} l_x m_x = 1 \tag{6}$$

with

m_x = mean number of female offspring per female of age x,

l_x = probability of a female at birth being alive at any stated age x

Hulting *et al.*'s (1990) algorithm also computes the net reproductive rate with standard error

$$R_0 = \sum_0^\infty l_x m_x, \tag{7}$$

the mean generation time

$$G = \frac{\ln(R_0)}{r_m}, \tag{8}$$

and the finite rate of increase

$$\lambda = e^{r_m} \tag{9}$$

For both species, the 'Jackknife' estimates of r_m were related to temperature by fitting equation [2]. Thus, population development is explained, as done before, on the basis of enzyme kinetics. The r_m values of the two species on cowpea at the different temperatures were compared according to Hultin *et al.* (1990) using a t-test. Similarly, r_m estimates of *C. tomentosicollis* on cowpea were compared to those obtained on pigeonpea.

Results

Temperature influence on cohort parameters

Development time and its variability. The number of *C. tomentosicollis* and *C. shadabi* individuals which completed development at each nymphal instar varied with temperature (Tables 1 and 2). Egg to adult development times ranged from 11 to 54 days for *C. tomentosicollis* and from 16 to 69 days for *C. shadabi*, depending on temperature. At all temperatures and for both species, the egg stage lasted longest, followed by the fifth nymphal instar. The same observation was made by Egwuatu & Taylor (1977a) for *C. tomentosicollis* reared on pigeonpea. The temperature influence on the development rates of the eggs and nymphs is shown in Figs. 1A and 2A, while the model parameters [eq. 2] are given in Table 3. The developmental rates of *C. tomentosicollis* eggs and nymphs were slightly higher than those of *C. shadabi*. At 15 °C no development could be observed for both species. Developmental rates for *C. shadabi* eggs, and for the nymphal stages of both species, displayed a linear increase between 18° and 34 °C, while the rate for *C. tomentosicollis* eggs followed a curvilinear temperature-dependency (Figs. 1A, 2A). On pigeonpea, Egwuatu & Taylor (1977a) found a comparable linear response of *C. tomentosicollis* between 20°C and 34 °C. Below 18 °C and above 34 °C the rates rapidly declined in both species and showed a 'backward-J' shape described by Wagner *et al.* (1984). Considerable mortality occurred at these temperatures (Tables 1 and 2) which may have had a selective effect on the surviving individuals and their developmental rates (Campbell *et al.*, 1974). The shape of the model in these ranges compared favourably with the findings of Jackai & Inang (1992) who report 18.5 °C to be the lower and 40 °C the upper limit for *C. tomentosicollis* development. Such ambient temperatures are not unusual in southern Benin and other areas where the two species are present (e.g., Booker,

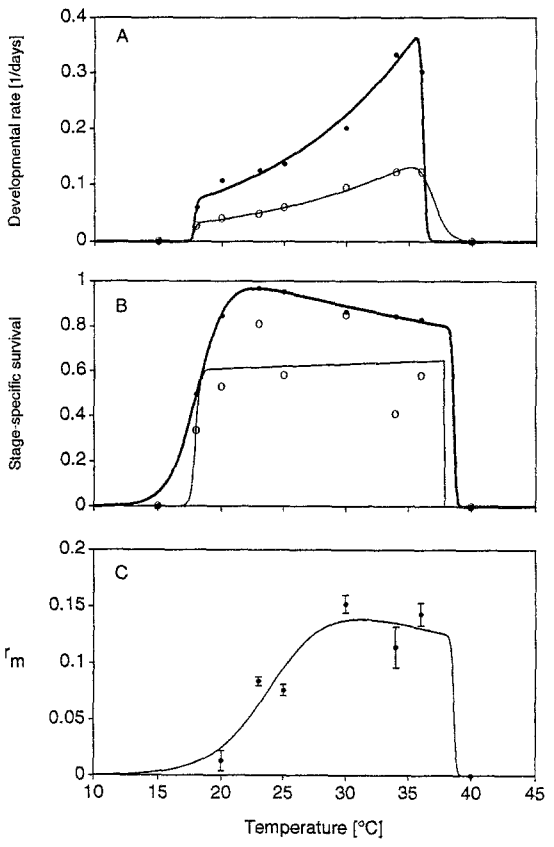

Fig. 1. Temperature influence on cohort parameters (A and B) and the intrinsic rate of increase r_m [d^{-1}] ('Jackknife' estimates, with associated standard error according to Hulting *et al.* (1990) (C) of *C. tomentosicollis* on cowpea pods. All observations fitted with the biophysical model of equation [2] (see text). —•— = egg stage, —o— = nymphal stage (instars 1–5 lumped together).

1965; Materu, 1971; Aina, 1975; Egwuatu & Taylor, 1977b,c). Thus, the model was useful for a realistic description of the temperature-dependency over a large range, including the extreme upper and lower temperatures.

The variability in the development times of the nymphal stages of the two species is depicted in Fig. 3. The distribution pattern of emergence times suggests that developmental rates vary among individuals and are probably a function of an individual's genetical characteristics (Curry & Feldman, 1987). By visual examination the Erlang density function [eq. 3], chosen on theoretical ground, appears to satisfactorily describe the variability in development. Nevertheless, the estimated values of the shape parameter H [eq. 3]

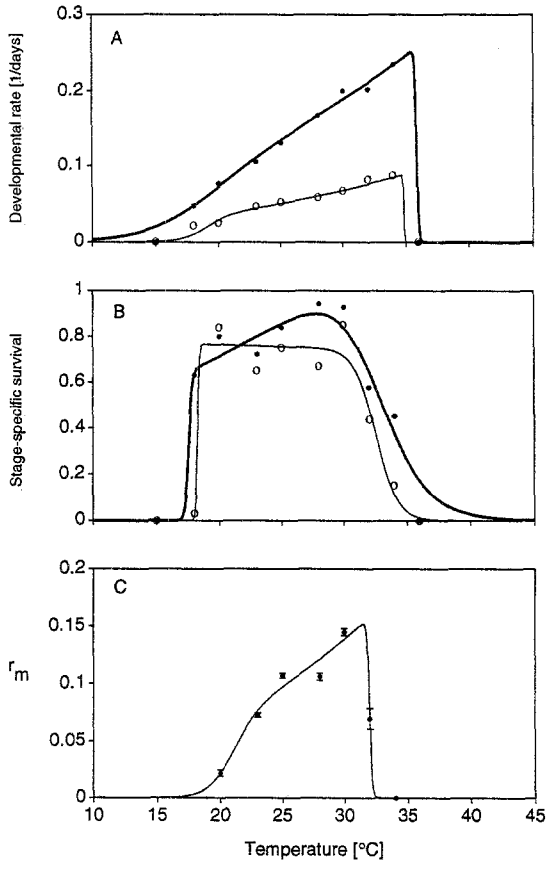

Fig. 2. Temperature influence on cohort parameters (A and B) and the intrinsic rate of increase r_m [d^{-1}] ('Jackknife' estimates, with associated standard error according to Hulting *et al.* (1990), C) of *C. shadabi* on cowpea pods. All observations fitted with the biophysical model of equation [2] (see text). —•— = egg stage, —o— = nymphal stage (instars 1–5 lumped together).

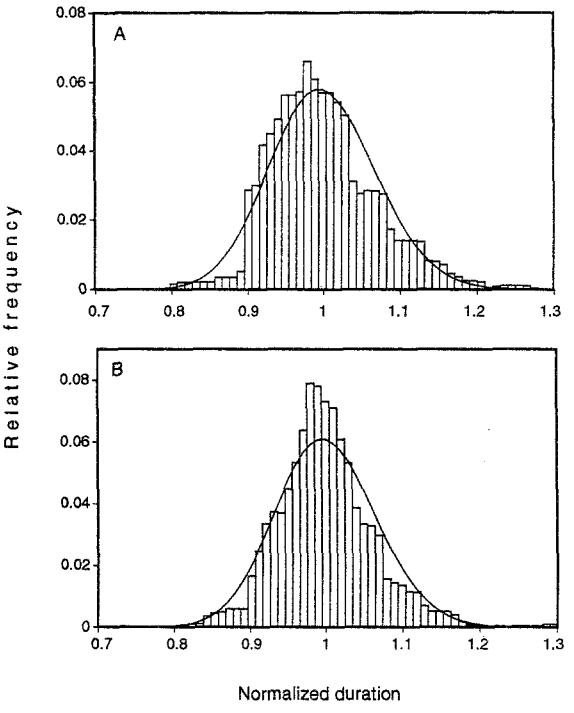

Fig. 3. Fit of the Erlang density function [eq. 3] to the observed frequency distribution of developmental times of nymphs of *C. tomentosicollis* (A) and *C. shadabi* (B). Mean developmental time is set equal to unity. Pooled data taken from several constant temperatures with low mortality.

for nymphs were high: 211 for *C. tomentosicollis* and 233 for *C. shadabi*.

Mortality. Total pre-imaginal survivorship as well as the survivorship of eggs and nymphs are given in Tables 1, 2 and 4. The temperature influence on the survival rates of the egg and the nymphal stages is shown in Figs. 1B and 2B. Corresponding model parameters (p1–p6, see eq. [2]) are presented in Table 3.

Egg survivorship of both species remained high between 20° and 30 °C (mostly >0.8). Above 30 °C, *C. shadabi* egg survivorship decreased (Table 2, Fig. 2B) and no eggs hatched at 36 °C, while 83% of the *C. tomentosicollis* eggs were still viable at this temperature. Apparently, eggs of *C. tomentosicollis*, which differ in shape and colour from eggs of *C. shadabi*, provide a better protection against hot temperatures due to some physiological difference. At 18 °C, *C. tomentosicollis* egg survivorship was reduced to about half, while 63% of the *C. shadabi* eggs hatched.

Nymphal survivorship between 20° and 30 °C ranged from 65% to 85% for *C. shadabi*, and from 53% to 85% for *C. tomentosicollis*. The survivorship of *C. shadabi* eggs and nymphs at high temperatures (>30 °C) was less than that of *C. tomentosicollis*. Only 15% *C. shadabi* nymphal survivorship was recorded at 34 °C, while at 36 °C 58% of the *C. tomentosicollis* nymphs survived (Figs. 1B and 2B). Due to high mortality (90%) of *C. shadabi* first instar nymphs at 18 °C, only 0.03% of the total nymphs survived at this temperature (Fig. 2B). At 18 °C, *C. tomentosicollis* nymphal survivorship was reduced to 34%. At 20 °C, however, survivorship of *C. shadabi* nymphs was higher (84%) compared to 53% survivorship of *C. tomentosicollis* nymphs. On pigeonpea pods, Egwu-

Table 4. Pre-imaginal survivorship ε and fertility parameters of the two pod sucking bug species *C. tomentosicollis* and *C. shadabi* on cowpea pods at different constant temperatures T_c (R_0 = net reproductive rate (± SE); G = mean generation time [in days]; λ = finite rate of increase)

	Clavigralla tomentosicollis					*Clavigralla shadabi*				
T_c [°]	R_0	SE (R_0)	G	λ	ε	R_0	SE (R_0)	G	λ	ε
15	--	--	--	--	0	--	--	--	--	0
18	0.40	--	88.9	1.01	0.17	0.10	0.14	83.43	1.00	0.02
20	1.73	0.78	53.9	1.01	0.45	5.53	1.45	79.69	1.02	0.67
23	52.84	6.85	47.5	1.09	0.79	46.69	5.01	52.78	1.08	0.47
25	14.04	2.70	35.1	1.08	0.55	128.08	10.79	45.27	1.11	0.71
28	--	--	--	--	--	68.30	9.25	39.75	1.11	0.63
30	39.96	6.87	24.3	1.16	0.73	101.63	11.22	31.85	1.16	0.79
32	--	--	--	--	--	7.48	1.63	29.13	1.07	0.25
34	8.78	3.24	19.7	1.12	0.71	0.74	0.21	26.25	1.00	0.07
36	14.84	2.96	19.0	1.15	0.48	--	--	--	--	0

atu & Taylor (1977a) found similar mortalities for *C. tomentosicollis* nymphs.

In general *C. tomentosicollis* survivorship was higher than *C. shadabi* at temperatures above 30 °C, while at the lower temperatures both species performed similarly.

The fit of the biophysical model [eq. 2] was less satisfactory than the fit to the developmental rate data. However, it accounts for the decreasing survival rates of both species at the upper and lower temperature extremes and shows a more comprehensive picture of the mortality pattern than other, e.g., linear temperature-rate models.

Fecundity and longevity. The age-specific fecundity of *C. tomentosicollis* (Fig. 4A) at 30 °C is well described by equation [5]. The following parameters were obtained: $c_1 = 4.886$, $c_2 = 0.885$, $c_3 = 1.16$ for *C. tomentosicollis* and $c_1 = 2.708$, $c_2 = 2.025$, $c_3 = 1.069$ for *C. shadabi*. A high variability in the number of eggs laid was observed for older (30–40 days after emergence) *C. shadabi* females. *C. tomentosicollis* females of the same age tended to lay fewer eggs at this temperature, which partly explains their lower fecundity (Tables 5 and 7).

The fecundity response to temperature [eq. 6] for both species on cowpea is depicted in Figs. 4B and 5B. The maximum fecundity of *C. tomentosicollis* is estimated at 28.6 °C, and that of *C. shadabi* at 26.3 °C. At 36 °C, a mean of 82 eggs per *C. tomentosicollis* female was recorded (Fig. 4B), whereas the fecundity of *C. shadabi* decreased after a maximum of 317 eggs

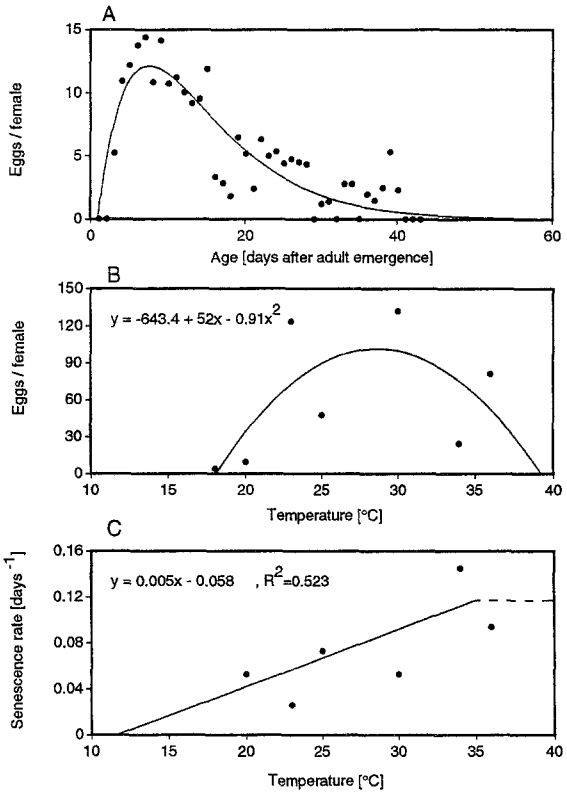

Fig. 4. Developmental attributes of *C. tomentosicollis* adult females on cowpea: age-specific fecundity at 30 °C, solid line resulting from equation [5] (A); fecundity response to temperature fitted by equation [4] (B); temperature-dependent senescence rates, fitted by linear regression, assumed to be constant after 35 °C (C) (see text).

Table 5. Fecundity and longevity of *C. tomentosicollis* females on cowpea at different temperatures (n = number of females)

Temperature		Eggs per female				
	n	Range	Mean	(± SE)	longevity	(± SE)
20 °C	20	0–47	9.3	± 4.15	11.7	±1.93
25 °C	30	0–172	47.7	± 9.18	13.6	±1.33
30 °C	30	0–385	132.2	±22.71	19.4	±2.11
34 °C	30	0–226	24.3	± 8.95	7.7	±1.24

Table 6. Fecundity and longevity of *C. tomentosicollis* females on pigeonpea at different temperatures (n = number of females)

Temperature		Eggs per female				
	n	Range	Mean	(± SE)	longevity	(± SE)
20 °C	30	0–20	1.5	± 0.89	21.7	±2.52
25 °C	30	0–128	16.2	± 6.23	12.1	±1.41
30 °C	30	1–538	213.1	±23.87	26.4	±2.30
34 °C	30	3–309	107.1	±15.05	24.4	±2.21

Table 7. Fecundity and longevity of *C. shadabi* females on cowpea at different temperatures (n = number of females)

Temperature		Eggs per female				
	n	Range	Mean	(± SE)	longevity	(± SE)
20 °C	30	0–104	16.0	± 4.19	24.0	±2.23
25 °C	30	38–555	316.6	±26.67	37.7	±2.34
30 °C	30	10–701	262.5	±29.01	27.9	±2.62
34 °C	30	0–103	18.5	± 5.37	11.9	±1.44

Table 8. Temperature-dependent senescence rate, $z(T_c)$ for *C. tomentosicollis* and *C. shadabi* on cowpea (cf. Figs. 4C and 5C)

Clavigralla species	$z(T_c)$	Temperature range
C. tomentosicollis	$0.005\ (T_c - T_o)$	$12\ °C < T_c < T_o = 35\ °C$
	0	$T_c < 12\ °C$
	$z(35\ °C)$	$T_c > T_o$
C. shadabi	$0.003\ (T_c - T_o)$	$12\ °C < T_c < T_o = 34\ °C$
	0	$T_c < 12\ °C$
	$z(34\ °C)$	$T_c > T_o$

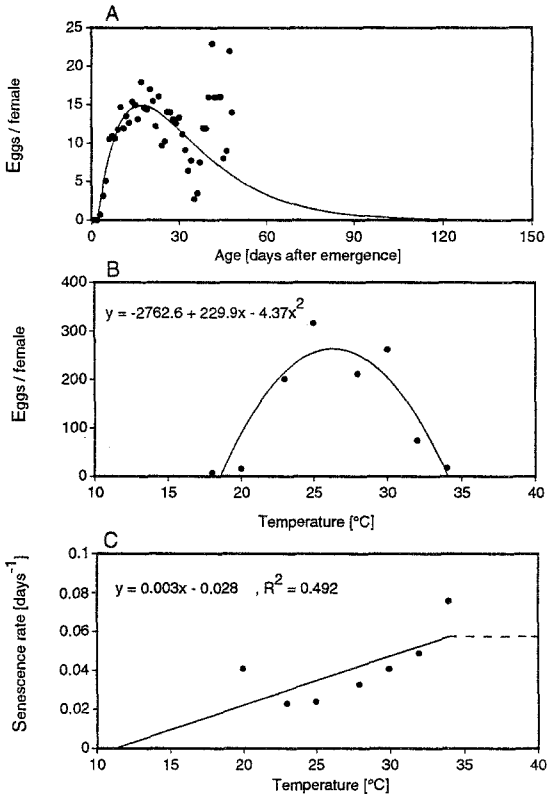

Fig. 5. Developmental attributes of *C. shadabi* adult females on cowpea: age-specific fecundity at 30 °C, solid line resulting from equation [5] (A); fecundity response to temperature fitted by equation [4] (B); temperature-dependent senescence rates, fitted by linear regression, assumed to be constant after 34 °C (C) (see text).

per female at 25 °C to 19 eggs per female at 34 °C (Fig. 5B, Table 6). For *C. tomentosicollis* the maximum possible temperature for oviposition is estimated at 39 °C, the lowest at 18.1 °C, while the upper and lower temperature limits of *C. shadabi* are estimated at 34° and 18.5 °C, respectively. In fact at 36 °C *C. shadabi* did not oviposit.

The mean longevity of *C. shadabi* females between 20° and 34 °C was slightly higher than that of *C. tomentosicollis*, which partly explains their higher fecundity (Tables 5 and 7). The longevity of both species was considerably shorter than reported elsewhere (Egwuatu & Taylor, 1977b; Materu, 1968) and may be due to confinement in Petri dishes and to different food sources.

The temperature effect on the ageing of females is shown in Figs. 4C and 5C. The senescence rate

is assumed to remain constant after a maximum is reached. The ageing of females is described in Table 8.

Temperature influence on demographic characteristics

Intrinsic rate of increase. The influence of temperature on the intrinsic rate of increase r_m of both species fed on cowpea is presented in Figs. 1C and 2C. The associated model parameters of equation [2] used to describe the response to temperature are specified in Table 3. The temperature range where the r_m value of *C. tomentosicollis* remains high is higher than that of *C. shadabi*. A maximum r_m for both species occurred at 30 °C, indicating that the maximal daily increase dN/dt in numbers N of *C. tomentosicollis* and *C. shadabi* will be the actual population size times a factor of 0.152 and 0.145, respectively. At 23 °C, the estimate for *C. tomentosicollis* ($r_m = 0.084 \pm 0.004$) was significantly (t-test, P = 0.05) higher than for *C. shadabi* ($r_m = 0.073 \pm 0.002$). Although the fecundity of *C. shadabi* was higher than that of *C. tomentosicollis* at this temperature, pre-imaginal mortality of the former was much higher (Table 4), resulting in a lower r_m value. Kiritani *et al.* (1963) demonstrated the influence of pre-imaginal mortality on the value of r_m for the pentatomid *Nezara viridula* L., in Japan. At 25 °C, on the other hand, the r_m for *C. shadabi* was significantly (t-test, P = 0.05) higher (0.107 ± 0.002) than that for *C. tomentosicollis* (0.076 ± 0.005). At this temperature, *C. shadabi* pre-imaginal survivorship and female fecundity were higher than those for *C. tomentosicollis* (Tables 5 and 7). At 34 °C, the r_m for *C. shadabi* was estimated to be zero, while that of *C. tomentosicollis* remained high until 36 °C when r_m was 0.143. This demonstrates the greater tolerance of *C. tomentosicollis* for higher temperatures.

The temperature effect on r_m of *C. tomentosicollis* reared on cowpea and pigeonpea is shown in Fig. 6. At 30° and 34 °C, the r_m values achieved on pigeonpea were significantly (t-test P = 0.05) higher than on cowpea. This partly reflects the higher fecundity of the insect on pigeonpea at these temperatures (Tables 5 and 6) and suggests that at such temperatures, which often occur in southern Benin, *C. tomentosicollis* population increases faster on pigeonpea than on cowpea. High populations on pigeonpea during the hot dry season in southern Nigeria have been reported by Egwuatu & Taylor (1983), who estimated 5–9 *C. tomentosicollis* generations per year. At 36 °C, on the other hand, the

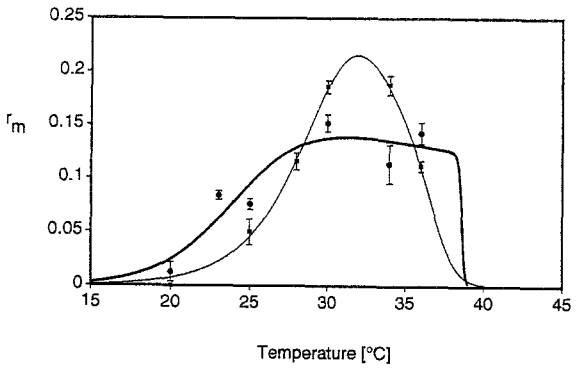

Fig. 6. Temperature influence on the intrinsic rate of increase r_m [d^{-1}] ('Jackknife' estimates, ± SE, according to Hulting *et al.* (1990)) for *C. tomentosicollis* on pigeonpea pods (—■—) and cowpea pods (—●—). Observations were fitted with the model of equation [2] (see text).

r_m obtained for *C. tomentosicollis* on cowpea was significantly (t-test, P = 0.05) higher than that obtained on pigeonpea. At lower temperatures, the r_m of the insect on cowpea was slightly but not significantly higher than on pigeonpea.

Other demographic characteristics. The relevant parameters indicated in Table 4 emphasize the high growth potential of the two species. At 30 °C, for instance, one generation of *C. tomentosicollis* will elapse in about 24 days and there will be an increase in numbers of 40 times, while *C. shadabi* will produce a generation in about 32 days that will be more than 100 times bigger than the preceding generation. The mean duration of a *C. shadabi* generation is usually greater than that of *C. tomentosicollis*, except at 18 °C, where *C. tomentosicollis* needs almost 3 months to complete one generation. Except at the high temperatures ($T_c \geq 34$ °C), the mean generation times was never below 20 days for either species.

The finite rate of increase, λ, shows the proportion of increase in number of females at a given temperature per day, with a maximum at 30 °C for both species (Table 4).

Discussion

The use of a biophysical model (Schoolfield *et al.*, 1981) proved adequate to describe the temperature-response of development, mortality and the intrinsic

rate of increase of both *C. tomentosicollis* and *C. shadabi*. It provides an excellent description of, in particular, development rates over a full range of temperatures. In general, *C. tomentosicollis* performance at high temperatures was better than that of *C. shadabi*, whose fecundity and longevity was higher at lower temperatures. This tendency agrees with the findings of Materu (1968) who pointed out that, in the Arusha area of Tanzania, *C. tomentosicollis* was more abundant during the hotter months, from August to March, with mean monthly minimum and maximum temperatures of 13° and 31 °C, respectively. On the other hand, he reported that *C. shadabi* was more abundant during the cool season (April–July), with mean monthly minimum and maximum temperatures of 13° and 25 °C, respectively.

The high H values obtained for the Erlang distribution function indicate an unexpectedly small variability in development times (see Shaffer, 1983) and suggest that a symmetrical distribution may be more appropriate to describe the variability. However, the data are not considered to be reliable enough for rejection of Erlang-distributed transit times (see Severini *et al.*, 1990). This is mainly because of the relative great interval between the observations (1 day) in respect to the total development time, *DEL*. A conclusive evaluation of the variability of *DEL* may only be feasible with smaller observation intervals. The Erlang distribution function takes account of the stochastic properties in development, an important characteristics of population ecology (Bellows, 1986a,b).

Oviposition period as well as fecundity were variable for both species and seem to depend at least in part on the type of food. Egwuatu & Taylor (1977b), for example, observed a long mean oviposition period (13 weeks) for *C. tomentosicollis* supplied with pigeonpea pods under insectary conditions with temperatures fluctuating between 25° and 32 °C. Materu (1968), on the other hand, recorded much shorter oviposition periods: five weeks for *C. tomentosicollis* and four weeks for *C. shadabi* when fed on the hyacinth bean, *Dolichos lablab* L., at 25 °C, which are comparable to observations in this study. Oviposition at the different temperatures was quite erratic, particularly for *C. tomentosicollis*. The same phenomenon was observed by Jackai (1989) for this species. At the intermediate and lower temperatures (18°–30 °C), *C. shadabi* displayed a higher fecundity than *C. tomentosicollis*. A similarly high fecundity of *C. shadabi* females was also found by Aina (1970) who reported a mean oviposition of 284 eggs per female, while Egwuatu & Taylor (1977b) gave a mean fecundity of 202 eggs per *C. tomentosicollis* female on pigeonpea under insectary conditions.

The comparison of r_m values of *C. tomentosicollis* on cowpea with those on pigeonpea suggests that, at temperatures around 32 °C, *C. cajan* (pigeonpea) is a more suitable host plant. This is important in explaining the population dynamics of this species on these two host plants, both widely distributed in West Africa.

Due to the assumption of a stable age distribution, the applicability of the r_m statistics to situations in practice is limited. However, it permits a comparison of the population growth potential between related species, or the comparison of an insect's performance on different food sources, as in the present case. The usual mean temperatures in southern Benin, mostly between 25° and 32 °C, are favourable for reproduction of both *C. tomentosicollis* and *C. shadabi* throughout the year. Nevertheless, the mean generation time suggests that under field conditions in southern Benin a second generation can hardly be expected before pod harvest of the cowpea variety used in this study, provided that oviposition starts at the podding stage of the plants. The population statistics given above illustrate the growth potential of each species, and provide a basis to explain their abundance under varying conditions such as temperature and food.

In conclusion, the results show the temperature-response of cohort parameters and demographic characteristics of two key pests of cowpea in Africa. At temperatures above 30 °C reproduction of *C. tomentosicollis* is significantly higher on pigeonpea than on cowpea and its development less restricted than that of *C. shadabi*. Since pigeonpea is present in many cowpea producing areas of tropical Africa, the findings underline the potential importance of this host plant for the build-up of *C. tomentosicollis* populations.

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