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BIONOMICS AND POPULATION GROWTH STATISTICS OF *CYRTOMENUS BERGI* (HEMIPTERA: CYDNIDAE) ON DIFFERENT HOST PLANTS

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ABSTRACT

Cyrtomenus bergi Froeschner (Hemiptera: Cydnidae) is a polyphagous subterranean burrower bug reported on various crops and weeds in the field. Bionomics and population growth statistics of *C. bergi* while feeding on peanut (*Arachis hypogaea* L.), pinto peanut (*Arachis pintoii*, Krapovickas et Gregory), maize (*Zea mays* L.), sorghum (*Sorghum bicolor* [L.] Moench), welsh onion (*Allium fistulosum* L.), and sweet and bitter cassava (*Manihot esculenta* Crantz) were calculated from development time, survival of immature stages, and reproduction and female longevity under laboratory conditions. Free-choice host plant selection among peanut, maize and sweet cassava was recorded with separate rearings of *C. bergi* from the different hosts. Optimal performance of *C. bergi* as measured by fecundity, survival, and intrinsic rate of population increase occurred on peanut and pinto peanut followed by maize. Sweet cassava, sorghum, and welsh onion were not favorable hosts, and *C. bergi* was unable to complete its life cycle on bitter cassava. In the free-choice test, insects reared on peanut and maize prior to the experiments were less active in their search for food, whereas insects reared on cassava prior to the experiment showed a clear preference for peanut and maize over cassava. Our results show that *C. bergi* is highly polyphagous, however, some host plants are strongly preferred over others. Cassava is not a preferred host and weeds in and around the cassava field may serve as alternative host plants that could maintain populations of *C. bergi* in cassava.

Key Words: Soil pest, cassava, maize, peanut, welsh onion, sorghum, *Cyrtomenus bergi*, Hemiptera

RESUMEN

Cyrtomenus bergi Froeschner (Hemiptera: Cydnidae) es un insecto barrenador subterráneo polífago que ha sido reportado en diversos cultivos y malezas en el campo. La bionomía y las estadísticas de crecimiento poblacional de *C. bergi*, mientras se alimentaba de maní (*Arachis hypogaea* L.), maní forrajero (*Arachis pintoii*, Krapovickas et Gregory), maíz (*Zea mays* L.), sorgo (*Sorghum bicolor* [L.] Moench), cebolleta (*Allium fistulosum* L.), yuca dulce y amarga (*Manihot esculenta* Crantz), se calcularon a partir de los datos sobre duración del desarrollo y supervivencia de las etapas inmaduras, reproducción y longevidad de las hembras en condiciones de laboratorio. Se registró la selección de plantas hospedantes en un ensayo de libre elección entre el maní, el maíz y la yuca dulce, empleando crías separadas de *C. bergi* de los diferentes hospedantes. Con base en los resultados de fecundidad, la supervivencia y la tasa intrínseca del aumento de población, el comportamiento óptimo de *C. bergi* se presentó en maní y en maní forrajero, seguido del maíz. La yuca dulce, el sorgo y la cebolleta no resultaron ser hospedantes favorables y *C. bergi* no pudo completar su ciclo de vida en la yuca amarga. En el ensayo de libre elección, los insectos criados en el maní y el maíz antes de los experimentos resultaron ser menos activos en la búsqueda de alimento, mientras que los insectos criados en la yuca antes del experimento mostraron una clara preferencia por el maní y el maíz respecto a la yuca. Los resultados indican que *C. bergi* es altamente polífago; sin embargo, este insecto muestra mayor preferencia por algunas plantas hospedantes que por otras. La yuca no muestra ser una planta hospedante preferida y malezas dentro y alrededor del cultivo de yuca pueda servir como planta hospedante alternativa manteniendo la población de *C. bergi* en la yuca.

Translation provided by the authors.

The subterranean burrower bug *Cyrtomenus bergi* Froeschner (Hemiptera: Cydnidae) is a polyphagous pest, reported in crops such as cassava (*Manihot esculenta* Crantz), maize (*Zea mays* L.), peanut (*Arachis hypogaea* L.), potato (*Solanum tuberosum* L.), onion (*Allium cepa* L.),

welsh onion (*Allium fistulosum* L.), sorghum (*Sorghum bicolor* [L.] Moench), African oil palm (*Elaeis guineensis* Jacq.), coffee (*Coffea arabica* L.), sugarcane (*Saccharum officinarum* L.), beans (*Phaseolus vulgaris* L.), peas (*Pisum sativum* L.), coriander (*Coriandrum sativum* L.), pastures and weeds (CIAT 1989, Cividanes et al. 1981, Lacerda 1983, Herrera 1988), and recently reported in asparagus (*Asparagus officinalis* L.) (Bellotti unpublished). *C. bergi* was first reported in welsh onion in 1974 (Higuita 1974, cited by Herrera 1988) and thereafter in maize (ICA 1980) and cassava (CIAT 1980). Since then, it has become a serious pest problem in regions throughout the neotropics (Bellotti et al. 1988).

All immature stages and the imago of *C. bergi* live in the soil. Oviposition also takes place there. Both adults and nymphs feed on roots, tubers and subterranean fruits (e.g., peanut) of the host plants leaving lesions in the plant tissue that facilitate the entrance of soil pathogens such as *Fusarium*, *Aspergillus*, *Genicularia*, and *Phytium* (CIAT 1980). On cassava, the infections appear as delimited dry rot spots (approx. 5 mm diameter) on the interior white starchy and edible parenchyma. Tissue degradation appears 12 to 24 h after feeding is initiated and is detectable when the root is peeled (García 1982). In cassava up to 85% of root damage (CIAT 1983) and up to 51% of starch reduction (CIAT 1985) can be ascribed to *C. bergi*. In maize, reddish spots appear at the feeding site and root rot and leaf chlorosis have been observed. A severe attack during early crop stages can cause wilting (King & Saunders 1984). In peanut both nymphs and adults pierce the pods and feed on the kernels. A light attack will cause delimited yellow to brownish dry rot spots (approx. 1.5 mm diameter) on the kernels of both mature and immature pods (Riis unpublished) and a severe attack can cause a complete decomposition of the harvest. Similar symptoms in peanut have been observed in Texas, USA, with the closely related Cydnidae, *Pangaueus bilineatus* Say (Smith & Pitts 1971).

It has not been possible to quantify damage due to *C. bergi* in the field in any of the reported crops apart from cassava where damage is assessed as a percentage of the parenchyma surface covered by rot spots. From a linear regression between percentage of cassava roots damaged and the number of *C. bergi* simultaneously collected at the same site during four crop cycles, Riis (1990) found 22% roots damaged when the number of *C. bergi* was close to zero (intercept, 22%), and the economic injury threshold was found to be 20-30% roots damaged (Bellotti et al. 1988).

An examination of life table parameters was conducted to obtain information on quality of a number of host plants. Experiments compare laboratory results on the development, survival, reproduction, and estimated life table parameters

for *C. bergi* while feeding on several host plants. Free-choice host selection tests for ovipositing females were conducted on females with different host plant experience.

MATERIALS AND METHODS

Stock Colonies

Cyrtomenus bergi was taken from stock laboratory colonies ($23 \pm 2^\circ\text{C}$, r.h. $65 \pm 5\%$, L12:D12) maintained on sprouting maize and peanut, respectively, in unsterilized soil (loamy clay) kept at a moisture level approximated to the field capacity (33.5% gravimetric soil water).

Experimental Host Plants

Fecundity, survival, and development were assessed on the following host plant diets: Sprouting peanut (*Arachis hypogaea* L. cv. Tatuí SM-76), pinto peanut (also called wild peanut, *Arachis pintoi*, Krapovickas et Gregory cv. Amarillo), maize (*Zea mays* L. cv. ICA V-156), and sorghum (*Sorghum bicolor* (L.) Moench cv. HW1758), root discs of a sweet cassava variety (*Manihot esculenta* Crantz cv. MCOL1468, < 100 ppm hydrogen cyanide measured), a bitter cassava variety (*Manihot esculenta*, Crantz cv. MCOL1684, ≥ 100 ppm hydrogen cyanide measured), and subterranean culms with primary roots of welsh onion (*Allium fistulosum* L.). Sprouting peanut, maize, and sorghum were placed in humid germination chambers 4 d before use. Cassava was harvested at the age of 7-12 months and chopped into 1 cm thick root discs. Welsh onions were bought from the local vegetable market and 3-cm culm, including primary roots, was provided to the insects.

Development Time and Survival of Immature Stages

Development time and survival of the five immature stages of *C. bergi* were assessed in a temperature and light controlled room ($25 \pm 1.5^\circ\text{C}$, r.h. $65 \pm 5\%$, L12:D12). To determine the nymphal development from hatching of eggs to adult, recently emerged (<16 h) first instars from the 'maize colony' were placed individually in approximately 30 cm³ soil (loamy clay, approx. 33% soil water content) in opaque plastic vials (55 cm³). One hundred individuals were placed on each host plant diet. Every 2 d the plant diet was renewed and the soil of each plastic vial was searched for exuviae until all nymphs had molted to the adult stage. Mortality of each instar and the number of days required to complete each life stage were recorded. Since observations were made every 2 d, subtracting 0.5 d approximated the development time of each life stage. An analysis of variance and subsequent REGWQ grouping (SAS Institute 1988) was computed for the

development time of each instar to facilitate comparisons among host plant diets.

Reproduction and Female Longevity

Fecundity and post-teneral female longevity were assessed for each experimental host plant diet ($25 \pm 1.5^\circ\text{C}$, r.h. $65 \pm 5\%$, L12:D12) with cohorts of 25-30 adult females recovered at ecdysis (<16 h after) from the 'maize colony'. This was repeated on the experimental peanut diet with insects from the 'peanut colony'. Each couple (1♀:1♂) was placed separately in approx. 50 cm³ soil (loamy clay, approx. 33% soil water content) in opaque plastic vials (55 cm³). Female survival was assessed every 2 d and the food diet was replaced at the same time. Dead males were replaced with males from stock colonies. Fecundity was assessed every 2 weeks. After transferring each couple into a new plastic vial with new soil, each old soil sample, representing oviposition of two weeks, was separately poured into 20% salt solution and the eggs floated off for recovery and counting (Matte-son 1966). Egg fertility (% eggs hatched) and pre-closure period were recorded from random samples of 50 eggs (four replications; total of 200 eggs) deposited by approx. 25 females at the age of 30-100 d after adult emergence when feeding on each of the host plant diets.

Statistics

From the survivorship and fertility schedules, the following bionomical statistics were calculated (Birch 1948; Carey 1993; Hulting et al. 1990).

Net reproductive rate (R_0):

$$R_0 = \sum_{x=0}^{\infty} l_x \cdot m_x \tag{1}$$

is the average number of newborn offspring produced by an average female during one generation calculated as the sum of realized fecundity of all age x , where l_x denotes the fraction of surviving females at age x and m_x denotes the age-specific birth rate.

Intrinsic rate of increase (r_m):

$$N_t = N_0 \cdot e^{r_m \cdot t} \tag{2}$$

is the instantaneous rate of change of population size of an exponentially growing population expressed in numbers per unit time (day⁻¹) per individual. We approximated r_m by the iterative method to the solution of the Lotka equation (Hulting et al. 1990):

$$\sum_{x=0}^{\infty} e^{-r_m \cdot x} l_x m_x = 1 \tag{3}$$

Finite rate of increase (λ):

$$N_t = N_0 \cdot \lambda^t \tag{4}$$

is the rate at which the population increases (geometrically) per individual per unit time (day⁻¹), i.e.,

$$\lambda = e^{r_m} \tag{5}$$

Generation time (T) (days):

$$R_0 = 1 \cdot e^{r_m \cdot T} \tag{6}$$

$$T = \frac{\ln R_0}{r_m} \tag{7}$$

is the average maternal age at which offsprings are born. For an exponentially growing population of iterative offspring producers the generation time (T) can be calculated from the equation of exponential populations growth (Equation 2) by setting the initial population size to one female ($N_0 = 1$). After one generation (T), the population size is equal to the net reproductive rate ($N_t = R_0$), see equations 6 and 7.

Population doubling time (D) (days):

$$N_t = N_0 \cdot 2 \tag{8}$$

$$\lambda^t = 2 = (e^{r_m})^t \text{ or } (e^{r_m})^D = 2 \tag{9}$$

$$D = \ln 2 / r_m \tag{10}$$

is the time required for the population to double which can be calculated from the equation of geometric increase (equation 4) when $t = 2$, see equations 8, 9 and 10.

Data on development time and survival of immature stages were included in the above calculations. Calculations were based on a sex-ratio of 1:1, which has been found in fields of both peanut and welsh onion from determining the sex of a total of 1833 adult individuals at three localities (Riis unpublished). Calculations were also based on the assumption that the egg fertility of eggs deposited throughout the post-teneral female life span was constant.

An analysis of variance and subsequent REGWQ grouping (SAS Institute 1988) was accomplished for the post-teneral female longevity and the area under the m_x -curve (fecundity weighted by age) to facilitate comparisons among

host plant diets. Heterogeneity of error was addressed by transforming the data of female longevity, days^{0.5}, and fecundity, $\ln(\text{area}+1)$, and the null hypothesis $H_0: b = 0$ for Taylor's Power Law, $s^2 = a + \bar{x}^b$, was accepted for the transformed data.

Host Plant Selection

A free-choice host plant selection design was set up with ovipositing females from different host plant experience, i.e., reared on peanut, maize, and cassava, respectively, for one generation. Specially made triangular wood boxes (60 cm side length; 6 cm height) were filled with moist soil (33% soil water). A triangle consists of four sub-triangles and each sub-triangle at each corner was filled with sprouting kernels of either peanut, maize, or root discs of a sweet cassava variety 'MCOL1468', respectively (Fig. 1). Three triangular boxes were set up simultaneously. One hundred females from each of the three rearing colonies were placed in the center of the triangle-sub-triangle, which did not contain a host plant (Fig. 1). The distribution of females and oviposited eggs were assessed after 24 h by calculating the number of females recovered in each sub-triangle. Soil from each sub-triangle was separately poured in a 20% salt solution and the eggs floated off for recovery and counting (Matteson 1966). The setup was repeated seven times with new females each time.

RESULTS

Development Time and Survival of Immature Stages

Cyrtomenus bergi can develop on a wide range of host plants (Table 1). The nymphal development time, however, differed significantly among hosts ($P < 0.0001$) (Table 1), and ranking according to shortest development time was peanut, pinto peanut << maize, sweet cassava, sorghum << welsh onion << bitter cassava. This ranking was consistent for each of the individual nymphal

stages, with exception of first and fifth instars. The development time of first instars did not differ significantly between the pinto peanut and sweet cassava hosts, neither did it differ significantly among maize, sorghum, welsh onion, and bitter cassava. The development time of the fifth instars did not differ significantly between the peanut and maize. The development time per instar increased significantly as the nymphs developed ($F = 290.8$, $df = 946$, $P < 0.0001$), however, second and third instar nymphs feeding on the peanut had shorter duration than first instars. The development time of fifth instars occupied 29-39% of the total nymphal development time. *Cyrtomenus bergi* was unable to complete its nymphal development on the bitter cassava variety MCOL1684.

Ranking according to nymphal survival was peanut, pinto peanut >> maize >> welsh onion > sweet cassava, sorghum >> bitter cassava. Almost complete survival occurred for nymphs feeding on peanut (98%), whereas all nymphs feeding on bitter cassava died prior to the fifth instar. In general, mortality was highest in the first instar and decreased with development. Relatively high mortality occurred during the fifth instar for nymphs feeding on sweet cassava (8%) and during the third instar on sorghum (9%) (Table 1).

Female Longevity

Survivals of post-teneral females are illustrated in Fig. 2. Longevity while feeding on the different host plants differed significantly ($P < 0.0001$) (Table 2), and ranking according to increasing longevity was peanut, pinto peanut > sweet cassava > maize >> bitter cassava.

Reproduction

Eggs are deposited singly in the soil. Age-specific fecundity is illustrated in Fig. 3. Total fecundity per female differed significantly among host plants ($P < 0.0001$) (Table 2), and ranking according to increasing progeny per female was peanut, pinto peanut > maize > sweet cassava >> bitter cassava. Females reared on peanut prior to the experiment and subsequently feeding on peanut and pinto peanut showed major ovipositional peaks at 70 and 100 d after adult emergence, respectively. Additional peaks were observed three to four times during the female life span (Fig. 3a). Females reared on maize prior to the experiment and subsequently feeding on peanut showed a major ovipositional peak slightly later at approx. 125 d after adult emergence and only two additional ovipositional peaks during the female life span at approx. 250 and 335 d after adult emergence (Fig. 3b). Females reared on maize or sweet cassava also showed a major ovipositional peak at approx. 125 d after adult emer-

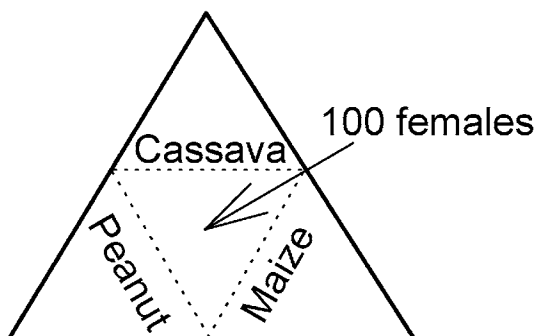


Fig. 1. Free-choice host selection design.

TABLE 1. DEVELOPMENT TIME (DAYS) AND MORTALITY (%) OF INSTARS OF *CYRTOMENUS BERGI* ($N_0 = 100$) WHILE FEEDING ON DIFFERENT HOST PLANTS.

Feeding history ¹	Experimental host plant	1 st		2 nd		3 rd		4 th		5 th		Total of all immature stages	
		Days ²	%	Days	%	Days	%	Days	%	Days	%	Days	%
Maize	Peanut	9.9 ± 0.13 a ³	0	7.6 ± 0.17 a	0	9.3 ± 0.16 a	0	10.8 ± 0.20 a	0	24.6 ± 0.26 a	2	62.4 ± 0.48 a	2
Maize	Pinto peanut	11.0 ± 0.34 ab	0	10.1 ± 0.35 a	0	9.3 ± 0.28 a	2	12.0 ± 0.31 a	0	23.0 ± 0.31 a	0	65.3 ± 0.47 a	2
Maize	Maize	14.6 ± 0.26 c	25	15.6 ± 0.24 b	7	16.6 ± 0.27 b	7	18.2 ± 0.23 b	2	26.5 ± 0.40 ab	3	91.5 ± 0.58 b	38
Maize	Sweet cassava	12.0 ± 0.49 b	54	14.4 ± 0.82 b	0	17.2 ± 1.08 b	4	19.1 ± 1.30 b	0	28.6 ± 0.94 b	18	91.3 ± 2.83 b	64
Maize	Sorghum	14.0 ± 0.29 c	41	14.6 ± 0.40 b	2	16.0 ± 0.55 b	16	19.2 ± 0.46 b	2	27.5 ± 0.53 b	4	91.8 ± 1.14 b	64
Maize	Welsh onion	15.4 ± 0.36 c	34	19.2 ± 0.47 c	17	23.6 ± 0.47 c	11	24.5 ± 0.63 c	4	36.6 ± 0.74 c	6	119.3 ± 0.99 c	56
Maize	Bitter cassava	15.5 ± 1.35 c	83	26.7 ± 4.63 d	47	40.0 ± 3.00 d	78	—	100	—	—	—	100
ANOVA ⁴		$df = 302$ $F = 32.31^{****}$		$df = 267$ $F = 73.15^{****}$		$df = 239$ $F = 148.3^{****}$		$df = 234$ $F = 108.6^{****}$		$df = 222$ $F = 80.73^{****}$		$df = 18$ $F = 235.9^{****}$	

¹Feeding history prior to the experiment.

²Values are means standard errors. A single-classification analysis of variance was applied separately to each instar.

³REGWQ-grouping: Means with the same letter within the same column are not significantly different.

⁴**** denotes $P < 0.0001$.

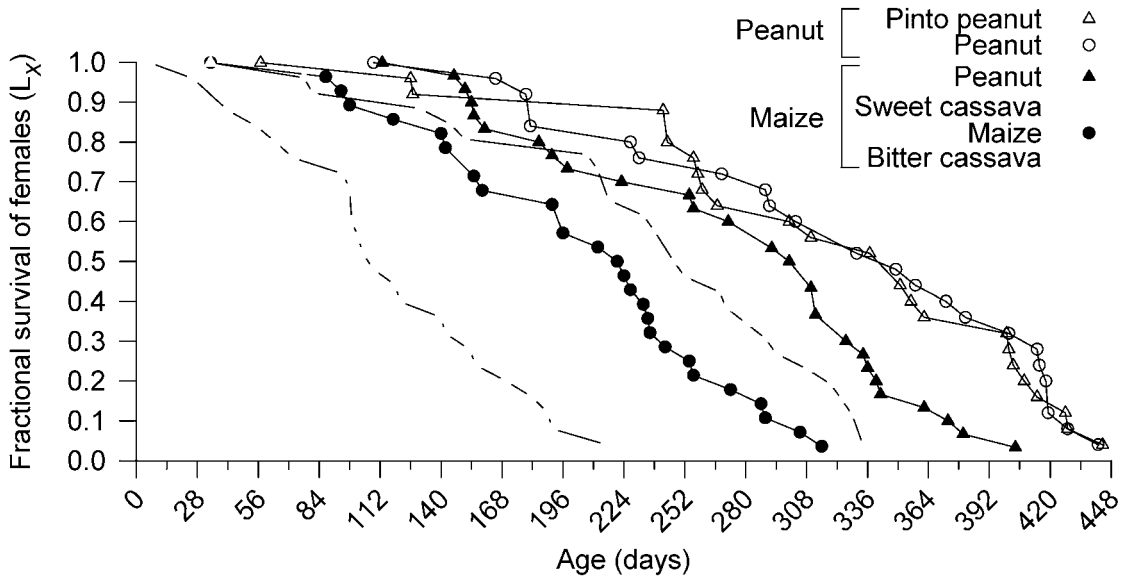


Fig. 2. Fractional age-specific survival of *Cyrtomenus bergi* females while feeding on different host plants (25°C), and after having been reared on peanut and maize, respectively, prior to the experiment.

gence, but oviposition remained high until approx. 200 d after adult emergence before oviposition eventually declined (Fig. 3b).

The ovipositional midpoint (50%) occurred at approx. 130 d after adult emergence while feeding on the peanut and maize, and at approximately 150 d after adult emergence while feeding on the

sweet and bitter cassava (Table 2), but the difference was not significant ($P < 0.7339$) (Table 2). Nevertheless, when these values were calculated as a percentage of adult female life span, a significant difference among host plants was observed ($P < 0.0001$) (Table 2). Females deposited 50% of their eggs in the first 40-45% of their adult life

TABLE 2. FEMALES LONGEVITY, TOTAL FECUNDITY PER FEMALES, PERCENT OVIPOSITING FEMALES, OVIPOSITIONAL MIDPOINT (50%), AND OVIPOSITIONAL MIDPOINT AS A PERCENTAGE OF ADULT FEMALE LIFESPAN OF *CYRTOMENUS BERGI* WHILE FEEDING ON DIFFERENT HOST PLANTS.

Feeding history ¹	Experimental host plant	n ²	Female longevity (days) ^{3,4}	Total fecundity per female (eggs) ^{3,5}	Ovipositing females	Ovipositional midpoint (50%) (days) ¹	Ovipositional midpoint as a percentage of adult female lifespan ¹
Peanut	Peanut	25	316.1 ± 19.9 a ⁶	224.1 ± 24.1 a	100%	127.4 ± 11.5 a	39.7% ± 2.0 a
Peanut	Pinto peanut	25	310.9 ± 20.6 a	252.4 ± 31.7 a	100%	133.7 ± 12.0 a	45.1% ± 3.4 a
Maize	Peanut	30	270.3 ± 15.0 ab	164.0 ± 20.7 ab	97%	136.2 ± 8.9 a	50.3% ± 1.8 ab
Maize	Maize	28	199.1 ± 13.6 c	93.0 ± 13.4 bc	93%	131.1 ± 9.3 a	64.6% ± 3.1 ab
Maize	Sweet cassava	26	232.2 ± 16.5 bc	52.3 ± 9.5 c	88%	150.3 ± 9.9 a	62.5% ± 3.9 ab
Maize	Bitter cassava	25	111.7 ± 11.0 d	1.3 ± 1.3 d	4%	153.0 ± 0.0 a	70.8% ± 0.0 b
Maize	Sorghum	—	—	—	—	—	—
Maize	Welsh onion	—	—	—	—	—	—
ANOVA ⁷			df = 153 F = 21.37****	df = 153 F = 67.31****		df = 123 F = 0.56 NS	df = 123 F = 11.47****

¹Feeding history prior to the experiment.

²n denotes sample size.

³Values are means ± standard errors.

⁴Single-classification analysis of variance was run on the number of days of longevity transformed as days^{0.5};

⁵Single-classification analysis of variance was run on the area under the m_x-curves transformed as ln(area+1);

⁶REGWQ-grouping: Means with the same letter within the same column are not significantly different.

⁷**** denotes P < 0.0001; NS denotes not significant.

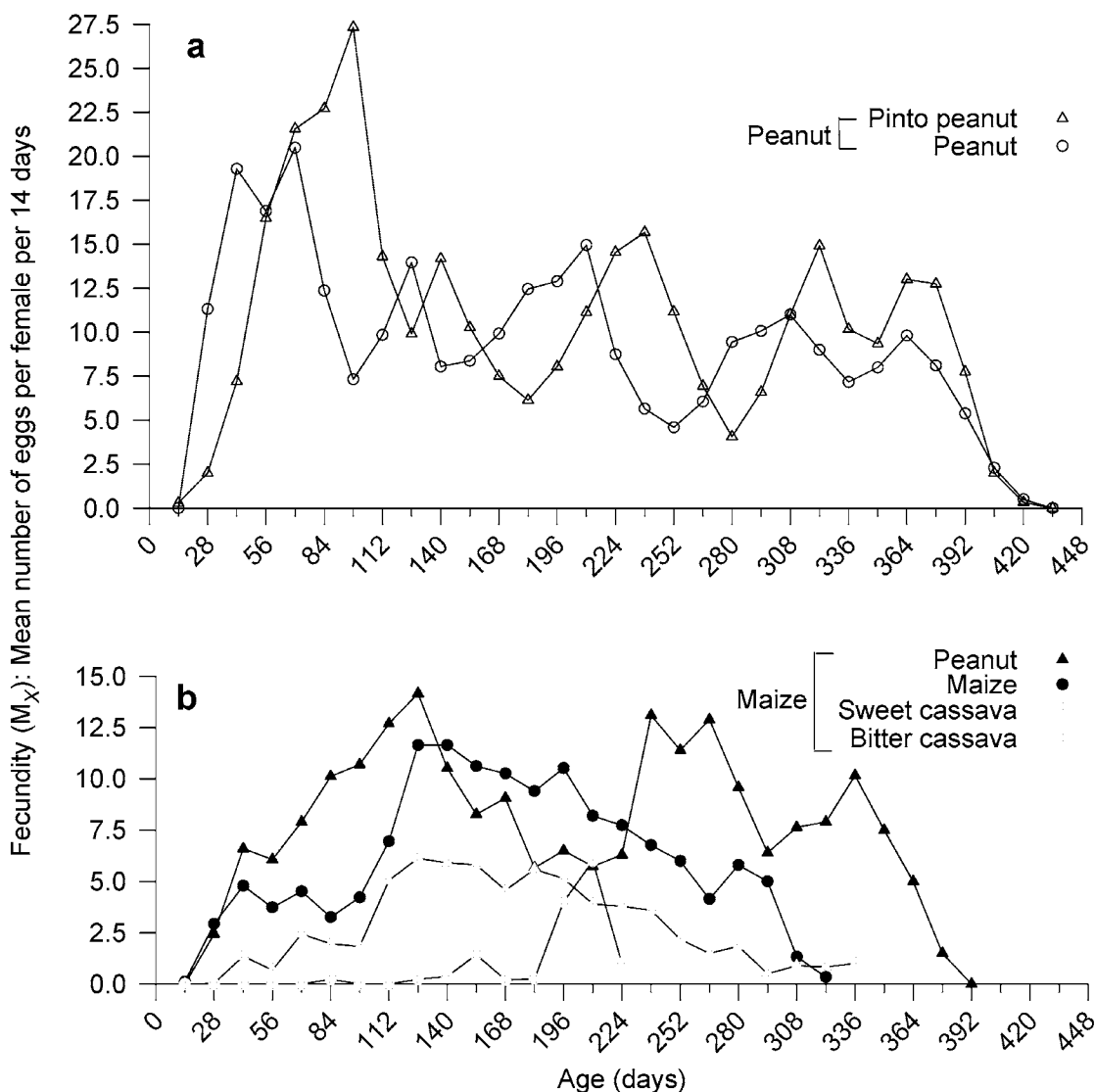


Fig. 3. Age-specific fecundity of *Cyrtomenus bergi* while feeding on different host plants (25°C), and after having been reared on peanut (a) and maize (b), respectively, prior to the experiment.

span when feeding on the peanut both before and during the experiment. When reared on maize prior to the experiment, females deposited 50% of their eggs within the first 50-65% of their life span while feeding on peanut, maize, and sweet cassava and within the first 70% of their life span while feeding on bitter cassava.

The pre-oviposition period ranged between 14-28 d on all hosts with exception of the bitter cassava, where only one female deposited eggs after 84 pre-ovipositional days (Table 3). Mean egg fertility was 90.5% and mean egg eclosion time was 13.5 d. Neither egg eclosion time nor mean egg fertility differed significantly among the host plants.

Population Growth Statistics

All life-table parameters with exception of egg fertility and eclosion time were found to be dependant on the host plant (Table 3). Net reproductive rate (R_0) was greatest for pinto peanut followed by peanut, and declined considerably for maize and sweet cassava. The intrinsic rate of increase (r_m) was significantly higher for females feeding on peanut, after pre-experimental rearing on peanut (Table 3) than after pre-experimental rearing on maize. For females reared on maize, the ranking according to increasing r_m -value was peanut >> maize >> sweet cassava. The values of doubling time (D) and mean generation time (T) decreased

TABLE 3. DEMOGRAPHIC PARAMETERS FOR *CYRTOMENUS BERGI* FEEDING ON DIFFERENT HOST PLANTS AT 25°C.

Feeding history ¹	Experimental host plant	n^2	Net reproductive rate (R_0) ³	Intrinsic rate of increase (r_m)/day ⁴	Finite rate of increase (λ)/day ⁵	Doubling time (D) (days) ⁵	Mean generation time (T) (days) ⁵
Peanut	Peanut	25	98.8 ± 10.6	0.0318 ± 0.0009 a ⁶	1.0323	22.0	145
Peanut	Pinto peanut	25	111.2 ± 14.0	0.0290 ± 0.0011 a	1.0294	23.8	162
Maize	Peanut	30	72.3 ± 9.2	0.0250 ± 0.0009 b	1.0254	27.6	170
Maize	Maize	28	25.9 ± 4.6	0.0154 ± 0.0015 c	1.0155	44.8	210
Maize	Sweet cassava	26	8.5 ± 1.5	0.0087 ± 0.0009 d	1.0088	77.7	240
Maize	Bitter cassava	25	—	—	—	—	—
Maize	Sorghum	—	—	—	—	—	—
Maize	Welsh onion	—	—	—	—	—	—

¹Feeding history prior to the experiment.

² n denotes sample size.

³Values of the net reproductive rate are means ± standard errors.

⁴Values of the intrinsic rate of increase are based on estimates of r_m ± standard error of Jackknife estimates (Carey 1993).

⁵Values of the finite rate of increase, doubling time and mean generation time are means.

⁶Means that lie within the 95% confidence interval of other means have the same letter.

as the intrinsic rate of increase (r_m) increased (Table 3).

Host Selection

Within a time frame of 24 h, higher numbers of ovipositing females, which were reared on peanut ($P < 0.0001$) and maize ($P < 0.0018$), remained at the release point, where no host plant was available, rather than moving to spaces with hosts (Table 4). On the contrary, females reared on sweet cassava preferred peanut and maize over sweet cassava ($P < 0.0001$), and proportionally more females moved towards the two preferred hosts

rather than staying at the release point with no host plants available (Table 4).

The distribution of oviposited eggs within the experimental space corresponded with the distribution of the females. Oviposition of females reared on peanut was high. Oviposition of females reared on maize and sweet cassava was low and there were no differences among hosts (Table 4).

DISCUSSION

Our results confirm that *C. bergi* is highly polyphagous. It can develop on a range of host plants from different families, but some host

TABLE 4. HOST PLANTS SELECTED BY 15-30 D OLD OVIPOSITING FEMALES OF *CYRTOMENUS BERGI* ($N = 100$) 24 H AFTER RELEASE IN A HOST PLANT FREE SPACE (SEE FIG. 1). THE SPECIMENS WERE TAKEN FROM THREE DIFFERENT COLONIES IN WHICH THEY FED ON PEANUT, MAIZE, AND SWEET CASSAVA, RESPECTIVELY, FOR ONE GENERATION PRIOR TO THE EXPERIMENT.

Host plant selected by <i>C. bergi</i> :	Pre-experimental colony					
	Peanut		Maize		Sweet cassava	
	Females	Eggs	Females	Eggs	Females	Eggs
Release point ¹ (no host plant)	56.5 ± 10.1 a ³	39.0 ± 9.3 a	50.3 ± 11.2 a	24.0 ± 9.1 a	20.7 ± 4.0 ab	18.8 ± 6.4 a
Peanut ²	17.9 ± 5.0 b	10.2 ± 3.8 b	21.3 ± 5.7 b	8.7 ± 5.3 a	33.4 ± 2.1 a	7.2 ± 2.8 a
Maize ²	16.1 ± 4.2 b	8.0 ± 2.1 b	18.3 ± 4.4 b	7.8 ± 3.7 a	32.6 ± 2.0 a	10.7 ± 3.8 a
Sweet cassava ²	9.3 ± 2.2 b	10.7 ± 3.5 b	9.9 ± 2.1 b	10.7 ± 3.6 a	13.1 ± 3.1 b	9.8 ± 3.7 a
ANOVA ⁴	$df = 24$ $F = 12.18^{****}$	$df = 24$ $F = 10.38^{****}$	$df = 24$ $F = 6.77^{**}$	$df = 24$ $F = 2.31$ NS	$df = 24$ $F = 11.21^{****}$	$df = 24$ $F = 1.85$ NS

Values are means of numbers of females located within each space ± standard errors;

Single-classification analyses of variance were applied separately to each group of host plant regime before test;

¹Insects were released in the central 'sub-triangle-space' of a triangle;

²The 'sub-triangle-space' of one corner in a triangle;

³REGWQ-grouping: Means with the same letter within the same column are not significantly different.

⁴**** denotes $P < 0.0001$; ** denotes $P < 0.001$; NS, not significant.

plants are strongly preferred over others. Best performance of *C. bergi* measured as fecundity, survival, and intrinsic rate of population increase, occurred on peanut and pinto peanut followed by maize. Sweet cassava, sorghum, and welsh onion were not favorable hosts, and *C. bergi* was unable to complete its life cycle on bitter cassava. The computation of the intrinsic rate of increase (r_m) (day⁻¹) resulted in a clear differentiation of the host plant qualities, and also the impact of the feeding history prior to the experiment was highly significant. The intrinsic rate of increase was significantly higher for insects feeding on peanut after pre-experimental rearing on peanut than after pre-experimental rearing on maize. The development time of nymphs feeding on sweet cassava after pre-experimental rearing on maize was 91.3 d compared with 111.3 d after pre-experimental rearing on sweet cassava (García 1982).

Nymphal development was consistently completed with five instars. In general, the development time increased as the instars increased, however, on peanut the second and third instars developed faster than the first instars indicating a major plasticity of these intermediate instars.

Although the development time on maize was not significantly different from that on sweet cassava and sorghum, maize offered better host qualities than sweet cassava and sorghum due to higher survival; 62% on maize compared with 36% on sweet cassava and sorghum. In the field, Peairs and Carballo (1987) found higher numbers of *C. bergi* in maize as a monoculture and in a maize-cassava intercropping than in cassava monoculture. Unfortunately, they did not assess the damage caused by *C. bergi* to explain whether maize acts as a trap crop reducing damage to cassava intercropped with maize, or alternatively, whether the damage to cassava in the intercropping system increases due to increased population density of *C. bergi*.

The total average life spans (egg eclosion time + nymphal development time + female longevity) for *C. bergi* feeding on the two types of peanut were 360-380 d. Interestingly, the total average life span for insects feeding on maize was only 290 d compared with 324 d for insects feeding on sweet cassava after pre-experimental rearing on maize in spite of the reproduction being higher on maize than on sweet cassava. Reduced reproduction and increased longevity while feeding on cassava compared with maize demonstrates a possible physiological trade-off between reproduction and longevity consistent with the 'principle of allocation' paradigm (Pianka 1988). The increase in life span caused by dietary restriction can be explained as a consequence of lower reproduction. This response may enable *C. bergi* to adapt increased fitness when encountering favorable food supply. García (1982) found that *C. bergi* had a greater total average life span of 418 d when feed-

ing on root discs of sweet cassava after pre-experimental rearing on cassava. However, García (1982) did not collect data on fecundity from the same females for comparison. Evidently the quality of peanut as a host plant can maintain both high reproduction and an extended longevity.

The total average fecundity when feeding on bitter cassava was almost zero; only one female out of 25 deposited eggs. The total average fecundity was twice as high when feeding on maize and three times higher when feeding on peanut compared with that of cassava. The pre-experimental rearing history had a significant impact on the fecundity; females feeding on peanut deposited 37% more eggs after pre-experimental rearing on peanut than after pre-experimental rearing on maize. The total average fecundity per host plant increased with increasing proportion of females depositing eggs.

The ovipositional midpoint as a percentage of adult female life span, however, differed significantly among hosts; the higher fecundity, the earlier in the life span the eggs were deposited resulting in a shorter mean generation time (T). The doubling time (D) of populations reared and feeding on peanut was twice as short as that of populations reared and feeding on maize and nearly four times shorter than the doubling time of populations feeding on sweet cassava. The daily population growth ranged from 3.2% in peanut to 1.5% in maize and 0.9% in sweet cassava.

The majority of the insects that had been reared on peanut and maize prior to the free-choice test remained in the release space where no host plant was available. On the contrary, insects reared on cassava prior to the test showed a clear preference for peanut and maize over cassava and the host plant free space where they had been released. Only females reared on peanut deposited sufficient eggs to reflect the female positioning and host selection. These results show a strong preference for peanut and maize. They also show that insects which have fed on peanut and maize are less active in their search for food; they are probably well fed and better prepared to survive in a host plant-free space or period of time. After rearing on peanut and subsequently left to starvation, Riis (unpublished) found the lethal time at 50% mortality to be 80 d for females and 74 d for males, demonstrating a strong capacity for survival in the absence of food. Unfortunately, the study did not include other host plants nor was the fecundity studied under these circumstances.

Our results show that cassava is not a preferred host to *C. bergi*, and insects fed on cassava are very active in their search for more and better food. In addition to this, Riis (1990) found that the thickness of the root peel is an obstacle to the propagation of *C. bergi*; first and second instars were unable to feed on un-peeled roots with a peel thickness greater than 2 mm, and only 3.3% of

first instars survived on roots with 1-1.5 mm thin peel. This may be one explanation to why the root apices, with thinner peel, were more frequently attacked and damaged than other parts of the root (Bellotti unpublished). In the case of cassava, we suggest that weeds in and around the cassava field may serve as alternative host plants that could maintain populations of *C. bergi* in cassava.

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