Abridged Life Tables for *Cephalonomia stephanoderis* and *Prorops nasuta* (Hymenoptera: Bethylidae) Parasitoids of *Hypothenemus hampei* (Coleoptera: Curculionidae: Scolytinae) Reared on Artificial Diet

Maribel Portilla\(^1\) and Michael Grodowitz

U.S. Department of Agriculture, Agricultural Research Service, Stoneville, MS 38776, and \(^1\)Corresponding author, e-mail: Maribel.portilla@ars.usda.gov

Received 29 November 2017; Editorial decision 27 January 2018

Abstract

Biological aspects and demographic parameters of *Cephalonomia stephanoderis* Betrem (Hymenoptera: Bethylidae) and *Prorops nasuta* Waterston (Hymenoptera: Bethylidae) parasitoids of the coffee berry borer (CBB), *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae) were investigated using diet-reared CBB hosts. Developmental time from eggs to adults, oviposition, and postoviposition period were comparable for both parasitoids. However, *P. nasuta* had a considerably longer preoviposition and longevity period averaging 17.3 and 63.1 d, respectively. The reproductive rate for *C. stephanoderis* was 46.1 daughters per female with a mean generation time of 474 d, whereas *P. nasuta* had a reproductive rate of 18.3 daughters per female in a mean time of 58.6 d. Oviposition behavior was also different with *C. stephanoderis* typically ovipositing on CBB prepupa and pupae, while *P. nasuta* preferred prepupa and second-instar CBB larvae. An abridged cohort life table for both parasitoids was constructed for growth rates estimations.

Key words: Cenibroca diet, *Cephalonomia stephanoderis*, *Prorops nasuta*, African parasitoids, life table

The coffee berry borer (CBB), *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae), is a key pest in coffee (*Coffeea arabica* L.) worldwide. Management of CBB has traditionally been accomplished through IPM including sampling and monitoring, cultural harvesting, postharvest control, pest management during ‘zoqueo’, use of *Beauveria bassiana*, and release of parasitoids (*Aristizabal et al. 2016*). A great interest exists in the potential for mass rearing of African parasitic wasps to reduce the damage produced by this pest. Among the most recognized biological control agents are the parasitoids, *Cephalonomia stephanoderis* Betrem (Hymenoptera: Bethylidae) and *Prorops nasuta* Waterston (Hymenoptera: Bethylidae). The practical use of *P. nasuta* and *C. stephanoderis* in biological control programs began in 1929 and 1988, respectively, *Murphy and Moore* (1990), *Portilla and Bustillo* (1995), *Bustillo et al.* (1996), *Portilla and Streett* (2008); *Portilla et al.* (2014); and *Vijayalakshmi et al.* 2014. The females enter the coffee berry and feed on CBB eggs, larvae, prepupa, and adults. It appears that females for both *C. stephanoderis* and *P. nasuta* must feed on larvae or prepupa in order to develop eggs (*Portilla and Streett* 2008). The preoviposition period for both species lasts for several days (*Murphy and Moore* 1990). *C. stephanoderis* eggs are normally oviposited on the ventral surface of CBB larvae and pupae and the dorso-abdominal region of the pupae. *P. nasuta* exhibited no marked oviposition site preference for deposition (*Abraham et al.* 1990; *Portilla et al.* 2014). Lateral-abdominal oviposition only on prepupa has been reported for *P. nasuta* (*Waterson 1923; Hargreaves 1926, 1935; Puzzi 1939, 1942; Abraham et al.* 1990; *Murphy and Rangi* 1991).
whereas pupae and prepupae have been reported for *C. stephanoderis* (Infante 1993, Portilla 1999a).

Mass production of these parasitoids is directly linked to CBB host production, and life tables for both parasitoid and pest are important to gain a better understanding on how to maintain equilibrium without a negative impact in one or both populations (Portilla et al. 2014). For example, complete and abridged life tables can be used for parasitoids depending on their oviposition behavior as endoparasitoids, ectoparasitoids, or if they attack single or multiple stages (Carey et al. 1988). There are a number of exceptions, including *C. stephanoderis*, and *P. nasuta*, that attack larvae, prepupa, pupae, and sometimes pharate adults (Portilla 1999a). *C. stephanoderis* and *P. nasuta* are idiobionts ectoparasitoids, which allow construction of complete cohort life tables. However, on the rate of increase and demographic parameters such as net maternity, there is little available information. Infante (1993) and Portilla (1999a) found that fecundity and survivorships were largely affected by the extremes of temperature; high mortality was found in immature stages for *C. stephanoderis* at 17°C, while at 37°C, all specimens died. The longevity was inversely related to temperature, although fecundity rate was reduced (Portilla 1999b).

Studies conducted in Colombia demonstrated that CBB could be controlled in commercial coffee farms using inoculative and inundative releases of the African parasitoid *C. stephanoderis*, when the infestation is lower than 5% (20 wasps every 2 mo per infested berry) (Salazar et al. 2002). Portilla (1999c) based on the results of Salazar et al. (2002) assessed approximately how many wasps should be used per releases by using a simulation model for improving ecological and economic recommendations for the control of the CBB in Colombia (Developed by Adrian Leach funded by The Department for International Development, United Kingdom) (Portilla 1999c). She gave the following example: The coffee harvest distribution of a hectare of 5,000 coffee trees with approximately 1,500 ripe berries per tree and 5% of CBB infestation would need about 4,400,000 ha (20 wasps per infested berry) to keep the CBB population under the threshold (2% of infestation). These wasps would be distributed through the year with releases every 2 mo as follow: February (260,000 wasps/ha), April (100,000 wasps/ha), June (480,000 wasps/ha), August (380,000 wasps/ha), October (2,000,000 wasps/ha), and December (1,200,000 wasps/ha). Producing those large numbers of parasitoids in a cost-effective way will depend on well-designed production facilities using industrial level mechanized and automated rearing processes only. Portilla 1999a and Portilla and Streett 2008 reviewed and discussed the requirements for a semiautomated system for mass production of CBB and its African parasitoids including diet preparation, sanitation, environmental factors, quality control, storage, and distribution. Unfortunately, no studies have examined calculation costs between the in vivo (naturally infested berries or parchment coffee methods) and the in vitro (artificial diet) rearing system for parasitoids production. However, to the best of our knowledge, no in vivo rearing system currently available will be able to supply such demand.

This study was conducted to obtain information on the biological parameters and fertility rates of these parasitoid species in an effort to get a better understanding how to improve our ability to rear large numbers for field release. Parasitoids were reared on CBB using Cenibroca artificial diet. Abridged cohort life tables for both parasitoids were constructed for growth rate estimations. Results are presented with tables and figures with a detailed description of all biological factors obtained by daily observations in life-table construction.

### Materials and Methods

#### Insect Colonies

This study was conducted at the USDA-ARS, Biological Control of Pests Research Unit (BCPRU), Starkville, MS. Adults of CBB and parasitoids were from colonies established in 1999 (Portilla et al. 2014) and maintained previously in the National Research Center of Coffee (CENICAFe) in Chinchina, Colombia. The colonies were shipped to the quarantine facility, Stoneville, MS, in 1999. The parasitoids and their host were reared according to the methods described by Portilla and Streett (2008). Rearing occurred in an environmental room with a photoperiod of 16:8 (L:D) h, 27°C (±1.5°C), and 55 (±10%) RH (Portilla 1999a). The Cenibroca diet was used to rear CBB and was prepared according to the procedures found in Portilla and Streett (2006).

#### Biological Parameters of *C. stephanoderis* and *P. nasuta*

Cohorts of 291 recently parasitized hosts by *C. stephanoderis* and 547 recently parasitized hosts by *P. nasuta* were used for this study. The size of cohort depended on availability. Each cohort was divided into 13 subcohorts (replicates) and placed into rearing containers (20 and 40 parasitized hosts per container, respectively) (Pioneer plastic 032C, Dixon, KY). They were held inside the environmental chambers (16:8 [L:D] h photoperiod, temperature of 25°C, and 55% RH) and kept until the last adult was obtained. Parasitized hosts were observed every day. Total number of parasitoids surviving from egg through adult and adult emergence was recorded on a daily basis for each species.

Twenty-five extra hosts recently parasitized by *C. stephanoderis* and *P. nasuta* were individually placed into Petri dishes 25 × 11 mm (Thermo Fisher 121V) and observed daily to determine egg, larva, prepupa, and pupa developmental time. From the 13 groups of each species, 15 copulated females were taken and individually confined into larger Petri dishes (35 × 11 mm) that contained 30 CBB immature stages (10 second-instar larvae, 10 prepupae, and 10 pupae) for oviposition as well as few eggs and first-instar larvae for feeding. The number of eggs oviposited every day by each parasitoid of both bethylids were counted and recorded until the last wasp was dead. Petri dishes were cleaned daily removing any dead or parasitized hosts and replacing them with new ones. Means of number of eggs oviposited per each female, longevity, pre-post, reproductive, and reproductive periods of *C. stephanoderis* and *P. nasuta* and their host preference for ovipositing were determined. The progeny of each female was maintained until adult emergence when sex ratio was determined.

#### Demographic Parameter of *C. stephanoderis* and *P. nasuta*

Abridged life tables for both species of parasitoid were calculated according to Portilla et al. (2014). Immature survival was calculated using the subcohorts for each parasitoid species. The fraction of death was calculated by the sum of all dead in each developmental stage and divided for the total beginning stages (synthetic cohort). This value was used for incorporating in the adult survival parameter \( l_0 \). Data obtained for the number of parasitic females alive each day at each age \( x \) and the number of eggs oviposited each day were used to calculate the basic population parameters: gross maternity \( M_x \), survival \( l_x \), fecundity \( m_x \), net maternity function \( l_x M_x \), net reproductive rate \( R_x \), finite rate of increase \( k \), intrinsic rate of increase \( r^* \), mean generation time \( T \), and doubling time \( DT \) (Krebs 2001, Pressat 1985, Carey 1993).
Statistical Analysis
One-way analysis of variance and the Tukey’s Honest Significant Difference test (SAS Institute, 2013) were used to compare life-table parameters, developmental time, preoviposition and oviposition period, longevity, immature mortality, and host preference. Nonparametric estimates of the survival function of females were compared between parasitoid species by using PROC LIFETEST test procedure in SAS (SAS 2013). Regression analysis was used to determine differences in cumulative gross fecundity between *C. stephanoderis* and *P. nasuta*.

Results

Biological Parameters of *C. stephanoderis* and *P. nasuta*

The percentages of host parasitized being offered equal numbers of second instar larvae, prepupae, and pupae of CBB of both parasitoids are presented in Fig. 1. *C. stephanoderis* had high percentages of parasitism in prepupae (60.85 ± 1.17 [SE]) followed by pupae (36.61 ± 11.28 [SE]) and only small populations of parasitized second-stage larvae were observed (2.52 ± 1.77 [SE]), whereas *P. nasuta* had a high preference for prepupae (50.29 ± 13.47 [SE]) followed by second-instar larvae (45.07 ± 14.72 [SE]) and occasionally parasitized pupae were observed (4.63 ± 3.15 [SE]). There were significant differences among preferences of parasitism percentage (df = 1, 28; *P* < 0.0001; *F* = 123.33, 5.49, 79.15 for second-instar larvae, prepupae, and pupae, respectively). The developmental time to egg (*F* = 80.93; df = 1, 48; *P* = 0.0001), larva (*F* = 11.19; df = 1, 48; *P* = 0.0016), and cocoon (*F* = 32.05; df = 1, 48; *P* = 0.0001) was significantly different among species. There were no statistical differences for prepupae (*F* = 0.05; df = 1, 48; *P* = 0.8295) and pupae (*F* = 0.91; df = 1, 48; *P* = 0.3437) between parasitoids (Table 1). Cocoons were formed in 2 d for both parasitoid species. No cocoons were formed in 51.65% of *C. stephanoderis* population and 42.46% of *P. nasuta*, but individuals still developed to adult maturity.

The proportion of death in each immature stage of *C. stephanoderis* and *P. nasuta* is presented in the Table 2. Using GLM analysis, parasitoids had a marked difference in survival between species for both eggs (*F* = 11.17; df = 1, 24; *P* = 0.0027) and pupae (*F* = 23.70; df = 1, 24; *P* = 0.0001), while no differences in survival were observed for larvae (*F* = 4.21; df = 1, 24; *P* = 0.0512) (Table 2). A comparison of female progeny production among species revealed that *C. stephanoderis* had a significantly higher reproduction than that of *P. nasuta* (*F* = 15.95; df = 1, 28; *P* = 0.0004). There were significant differences in female production per day (*F* = 151.85; df = 1, 940; *P* = 0.0001), where *C. stephanoderis* female were found ovipositing 2.22 ± 0.06 (SE) eggs/day/female and *P. nasuta* 1.21 ± 0.06 (SE) eggs/day/female. In general, both parasitoids species were normally found ovipositing from one to three eggs per day. However, sporadic ovipositions from four to seven eggs per day were observed for *C. stephanoderis* and from four to five eggs per day for *P. nasuta*. The number of eggs per wasp varied from 38 to 114 eggs for *C. stephanoderis* and 6 to 88 eggs for *P. nasuta*. Suggesting that it could be related to the amount of CBB stages provided during their entire life (about 300 CBB stages). Percentage of number of eggs oviposited per female among species is presented in Fig. 2. No *C. stephanoderis* population was found with <20 eggs per wasp and 0% of *P. nasuta* population had >100 eggs per parasitoid. In total, 20% of *C. stephanoderis* and 55% of *P. nasuta* population was found ovipositing 20–50 eggs per female, while 53% of *C. stephanoderis* and 20% of *P. nasuta* population was found ovipositing 50–100 eggs per female.

Both parasitic wasps had a different behavior on host parasitisation. *C. stephanoderis* oviposited a single egg per host and did not oviposit until the host was completely paralysed, whereas *P. nasuta* could oviposited more than one egg on host when they still moving, although the host have had various stinging. This behavior could explain the statistic differences found on their pre-reproductive period (*F* = 16.56; df = 1, 28; *P* = 0.0003) and longevity (*F* = 7.55; *P* = 0.0049), as well as total time to adult (**Table 1**).

**Table 1. Mean developmental time for the immature stages of *C. stephanoderis* and *P. nasuta* developed on diet-reared CBB hosts**

| Life stages | Developmental times (d) | (Mean ± SE) |
|-------------|-------------------------|-------------|
|             | *C. stephanoderis*      | *P. nasuta* |
| Egg         | 3.00 ± 0.58a            | 4.48 ± 0.49b|
| Larva       | 4.16 ± 0.84a            | 4.96 ± 0.63b|
| Cocoon      | 3.84 ± 0.62a            | 2.84 ± 0.51b|
| Prepupae    | 4.08 ± 0.65a            | 4.12 ± 0.53a|
| Pupa        | 13.60 ± 1.03a           | 13.32 ± 0.85a|
| Total time  | 28.68 ± 1.58a           | 29.72 ± 1.05b|

Means ± SE followed by the same letter in each row are not significantly different (*P* > 0.05, Tukey’s test) (*N* = 25 per species).

**Table 2. Immature stage mortality for *C. stephanoderis* and *P. nasuta* developed on diet-reared CBB hosts**

| Stages/parameters | Percentage immature mortality (mean ± SE), *C. stephanoderis* | Percentage immature mortality (mean ± SE), *P. nasuta* |
|-------------------|---------------------------------------------------------------|-----------------------------------------------------|
| Eggs              | 4.17 ± 4.08a                                                 | 12.33 ± 7.10b                                       |
| Larvae            | 11.09 ± 6.31a                                                | 17.93 ± 9.74a                                       |
| Pupa              | 1.4 ± 1.89a                                                  | 12.61 ± 7.53b                                       |
| Cumulative mortality | 16.12 ± 6.98a                                    | 36.31 ± 14.66b                                      |
| Survival to adulthood | 83.87 ± 6.42a                                | 63.69 ± 15.08b                                      |

Means ± SE followed by the same letter in each row are not significantly different (*P* < 0.05, Tukey’s test).
df = 1, 28; P = 0.0104). Preoviposition period (17.26 ± 10.57 d) and longevity (63.13 ± 13.23 d) were significantly longer for *P. nasuta* as compared to *C. stephanoderis*, (4.25 ± 0.43 and 46.66 ± 15.41 d). GLM showed no significant differences among parasitoids on reproductive (*F* = 0.83; df = 1, 28; *P* = 0.3706) and postreproductive periods (*F* = 3.98; df = 1, 28; *P* = 0.0559) (Table 3). During their postreproductive period both wasp species continued feeding upon their hosts. Both parasitoid species tended to produce more females than males, but their sex ratio varied among species. Total eggs deposited by *C. stephanoderis* and *P. nasuta* and sex ratio among parasitoids are presented in Table 4.

**Life-Table Parameter of *C. stephanoderis* and *P. nasuta***

Life-table data indicated differences between the two parasitoid species. For example, mean daily egg production (M.*) for *C. stephanoderis* increased to almost 4.0-fold during the first week and remained at high numbers of egg production until the end of the second week (Fig. 3A). Subsequently, the production of this parasitoid declined over the next 5- to 6-wk period reaching zero by about day 50. Alternatively, *P. nasuta* showed a constant trend in production from day 19 to day 45. Mortality, analyzed by the test of equality with *P. nasuta*.

Alternatively, *P. nasuta* showed a constant trend in production from day 19 to day 45. Mortality, analyzed by the test of equality with *P. nasuta*.

![Figure 2](https://example.com/figure2.jpg)

**Figure 2.** Population percentage of *C. stephanoderis* and *P. nasuta* oviposition number of eggs per female (n = 15 parasitoid females).

**Table 3.** Preoviposition, oviposition, and postoviposition periods, and longevity of *C. stephanoderis* and *P. nasuta* developed on diet-reared CBB hosts

| Periods                  | *C. stephanoderis* (Means ± SE) | *P. nasuta* (Means ± SE) |
|--------------------------|---------------------------------|--------------------------|
| Preoviposition           | 4.53 ± 0.43a                    | 17.26 ± 10.57b           |
| Oviposition              | 32.13 ± 13.16a                  | 28.40 ± 8.42a            |
| Postoviposition          | 11.00 ± 8.54a                   | 17.46 ± 8.58a            |
| Adult longevity          | 47.66 ± 15.41a                  | 63.13 ± 13.23b           |

Note: Means ± SE followed by the same letter in each row are not significantly different (*P* = 0.05, Tukey’s test) (N = 15 per species).

**Discussion**

The parasitic wasps *C. stephanoderis* and *P. nasuta* are idiobiont ectoparasitoids that attack every stage of CBB ovipositing on final-stage larvae (2.52 and 45.07%), prepupe (60.85 and 50.29%), and the pupal stages (36.61 and 46.39%), respectively, which is quite common among idiobiont ectoparasitoids (Shaw 1994). Both parasitoids preferred to feed on pupae rather than eggs or early instar larvae. The percentages of host preference obtained in this work differ from Barrera et al. (1989) and Abraham et al. (1990) who found that *C. stephanoderis* preferred ovipositing on pupae rather than prepupae. However, Infante (1993) observed 55.4% of eggs on prepupae and 44.6% on pupae. Portilla (1999) found similar results for *C. stephanoderis*, which was exposed to different temperatures.

There are two general forms of the life table, using original or hypothetical cohorts (Carey 1993). The first is the cohort life table, which provides a longitudinal perspective that includes the mortality experience of a particular cohort from the moment of birth through consecutive ages until no individuals remain in the original cohort. The second is the abridged life table, which assumes a hypothetical cohort subject throughout its lifetime to the age-specific mortality rates prevailing for the actual population over a specific period. Most aspects of the life history of *C. stephanoderis* and *P. nasuta* have been collected from studies carried out in captivity using a

**Table 4.** Total production and sex ratio of *C. stephanoderis* and *P. nasuta* developed on diet-reared CBB hosts

| Variable                  | Parastiods |
|---------------------------|------------|
|                           | *C. stephanoderis* | *P. nasuta* |
| Total eggs oviposited     | 1,101      | 540         |
| Total adult emerged       | 815        | 388         |
| Total females             | 702        | 302         |
| Total males               | 113        | 86          |
| Sex ratio                 | 6.2:1      | 3.5:1       |

Mean ± SE followed by the same letter in each row are not significantly different (*P* = 0.05, Tukey’s test) (N = 15 per species).
hypothetical cohort. This is because under normal circumstances, its complete life cycle is not feasible. Several studies have reported comparative data for different feeding regimes, temperatures, and some aspects of oviposition behavior and reproductive potential. Koch (1973) showed that *C. stephanoderis* has a developmental time of 23.2, 20.0, 15.2, and 14.6 d at 24, 27, 30, and 32°C, respectively. Also, the preoviposition time varied from 8.0 d at 21°C to 2.0 d at 27°C. However, 10 d at 17°C and 2 d at 32°C was the preoviposition period identified by Infante (1993). Portilla (1999) found that the preoviposition period occurred in 4.5 d at 23°C, 3.7, 2.9 and 2.1 d at 25, 27, and 29°C, respectively. Eggs hatch varied from 4.1 d at 23°C to 2.9 d at 29°C; Abraham et al. (1990) found that at 25°C eggs hatched in 1.61 d. Murphy and Rangi (1991) reported that *P. nasuta* needed 5.3 d for preoviposition and 30.6 d from egg to adult at 27°C and 75% RH. At 25°C and 90% RH, Abraham et al. (1990) obtained a preoviposition period of 14 d and development time of 22.4 d at 25°C.

The statistical analysis of the synthetic cohort used for *C. stephanoderis* and *P. nasuta* permitted the construction of abridged life-table functions, which were computed daily over their entire life. The development time from egg to adult did not vary appreciably from results obtained by different researchers with temperatures of 25°C. *P. nasuta* had a higher mortality value for every immature stage in comparison to *C. stephanoderis* (Table 2). The low mortality of *C. stephanoderis* is probably reflected in the ability of the female to select high-quality hosts (large and healthy) for oviposition, whereas *P. nasuta* was observed ovipositing eggs on larvae when the paralysis process was uncompleted. The capacity of predation of *P. nasuta* is another characteristic that impacts mortality, due to the female ovipositing eggs on the host where predation was initiated and even oviposited on small larvae. In effect, this type of stage selection does not provide all the resources necessary for its survival. These behavioral characteristics for *P. nasuta* provide a better understanding why this parasitoid has been difficult to rear under laboratory conditions. Portilla (1999a) reported only 28.4 stages per parchment coffee at 25 d after infestation, and from this population only a 29.09% has provided during their entire life (almost 300 CBB stages per female wasp). The same authors reported 14 d when *P. nasuta* was fed honey and there were no significant differences when fed CBB pupas and adults with no additional food. The authors reported 14 d when *P. nasuta* was fed CBB eggs and larvae. The larger longevity of *C. stephanoderis* and *P. nasuta* found in this study could be related to the amount of suitable hosts provided during their entire life (almost 300 CBB stages per female wasp). Fecundity ranges enormously in parasitic wasps and depends upon several factors, including species, size, and diet (Jervis and Copland 1996). Abraham et al. (1990) reported that female *C. stephanoderis* could lay 1–3 eggs and occasionally 4 per day and produce up to 70 eggs during her life. Barrera et al. (1989) found up to 9 eggs per parasitoid per day and the most fecund individual produced 139 eggs in 66 days.

### Table 5. Life-table statistic for *C. stephanoderis* and *P. nasuta* reared on *H. hampei* developed on diet-reared CBB hosts

| Parameters and units | Parasitoids |
|----------------------|-------------|
|                      | *C. stephanoderis* | *P. nasuta* |
| Gross fecundity (*Mx*) | 81.32 | 39.44 |
| Fecundity (*m*) | 67.99 | 31.09 |
| Net reproductive rate (*R*) | 46.15 | 18.33 |
| Mean generation time (*T*) | 47.39 | 58.60 |
| Doubling time (*DT*) | 7.78 | 13.12 |
| Intrinsic rate of increase (*r*) | 0.089 | 0.052 |
| Finite rate of increase (*λ*) | 1.09 | 1.05 |

*a* Total offspring/female.
*b* Females/female at age x.
*c* Daughters/new-born female (Population which increases each generation).
*d* Mean age of reproduction (d).
*e* Time required for (*λ*) to doubling number.
*f* Rate of natural increase (daughters/female/day).
*g* Individuals/female/day.

for preoviposition and 30.6 d from egg to adult at 27°C and 75% RH. At 25°C and 90% RH, Abraham et al. (1990) obtained a preoviposition period of 14 d and development time of 22.4 d at 25°C.

In captivity, and under good conditions, many wasp species will live 1 or 2 mo (Quicke 1997). Barrera et al. (1989) investigated the effect of adult diet on longevity of *C. stephanoderis*. He mentioned that longer longevity was found (77 d) when the adults were provided a honey-water mixture. However, Murphy and Rangi (1991) reported only 2 d for *P. nasuta* when fed honey and there were no significant differences when fed CBB pupas and adults with no additional food. The authors reported 14 d when *P. nasuta* was fed CBB eggs and larvae. The larger longevity of *C. stephanoderis* and *P. nasuta* found in this study could be related to the amount of suitable hosts provided during their entire life (almost 300 CBB stages per female wasp). Fecundity ranges enormously in parasitic wasps and depends upon several factors, including species, size, and diet (Jervis and Copland 1996). Abraham et al. (1990) reported that female *C. stephanoderis* could lay 1–3 eggs and occasionally 4 per day and produce up to 70 eggs during her life. Barrera et al. (1989) found up to 9 eggs per parasitoid per day and the most fecund individual produced 139 eggs in 66 days.
In this study, the numbers of eggs per *C. stephanoderis* varied from 34 to 114, and from 6 to 88 to *P. nasuta*. *C. stephanoderis*, on average, oviposited 81 eggs per wasp in 47.6 d and in comparison, *P. nasuta* oviposited 47 eggs in 63.1 d. These results indicate that under field conditions, females of *C. stephanoderis* and *P. nasuta* never obtain enough hosts to achieve full reproductive potential. Several studies confirmed that females always predominate in these two bethylides. The field sex ratio of the parasitic wasp *C. stephanoderis* recorded by Ticheker (1961) was 4.8 females per 1 male, and Koch (1973) found 2.7 females per 1 male. *Barrera et al.* (1993) obtained a sex ratio of 7:1 under laboratory condition, while Benassi (1998) found a *P. nasuta* a sex ratio of 5.2 females per male. This ratio varied through various generations, with 28.5 females per male after five generations. The sex ratio obtained in this work was 6.2: 1 and 3.5: 1 for *C. stephanoderis* and *P. nasuta*, respectively.

According to these results *C. stephanoderis* produced more females per female than *P. nasuta* (*R*.), but both parasitoids need at least 30 suitable host stages to assure progeny. The speed at which the colony increased (*R*.) is the most important parameter, and *C. stephanoderis* obtained a high intrinsic rate of increase. Mass production of both parasitoids depends on the host reproductive potential, and hence, these results provide insight as to why the parasitoids have been so unsuccessful in the field, because to proliferate they evidently need a range of host stages. If a wasp attacks an immature berry, it will encountered only eggs and young larvae which they may consume and kill the CBB female as well, but the female parasitoid will not produce any offspring (*Baker 1999, Ruiz-Cardenas and Baker 2010*). In addition, if the wasp arrives too late, they will find mostly adult CBB and have to wait until they start breeding, by which time harvest may intervene. All this suggests that *C. stephanoderis* and *P. nasuta* will be incompatible with efficient commercial production. However, we must consider studies that have demonstrated that a high number of wasps per hectare (20 wasps per infested berry every 6 mo) can control CBB or keep it under controls in plots with less than 5% of CBB infestation (*Aristizabal et al.* 1997, *Salazar and Baker* 2002, *Aristizabal et al.* 2011).

**Acknowledgments**

The authors would like to thank Luis Carlos Jojoa former technician at USDA, ARS, BCPRU, Starkville, for their valuable support in rearing the host and parasitoid colonies. We are also grateful to Carlos Blanco (SIMRU-ARS-USDA) and Arnudio Valencia (Nebraska University, Department of Entomology) for critically reviewing an early version of this manuscript.

**References Cited**

*Abraham, Y. J., D. Moore, and G. Godwin. 1990. Rearing and aspects of biology of *Cephalonomia stephanoderis* and *Prorops nasuta* (Hymenoptera: Bethylidae) parasitoids of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). Bull. Entomol. Res. 80:121–128.*

*Aristizabal, L. F., P. S. Baker, J. Orozco, and B. Chavez. 1997. Parasitismo de *Cephalonomia stephanoderis* (Betrem) sobre una poblacion del *Hypothenemus hampei* (Ferrari) con niveles bajos de infestacion en campo. Rev. Colom. Entomol. 23:157–164.*

*Aristizabal, L. F., P. S. Baker, J. Orozco, and B. Chavez. 1998. Efecto del parasitismo de *Cephalonomia stephanoderis* (Hymenoptera: Bethylidae) sobre las poblaciones de *Hypothenemus hampei* (Coleoptera: Scolytidae) durante y después de la cosecha. Rev. Colom. Entomol. 24:149–155.*

*Aristizabal, L. F., M. Jimenez, A. E. Bustillo, and S. P. Arthurs. 2011. Introduction of parasitoids of *Hypothenemus hampei* (Coleoptera; Scolytidae) on small coffee plantations in Colombia through farmer participatory methods development. Fla. Entomol. 94: 690–693.*

*Aristizabal, L. F. and A. E. Bustillo. 2016. Integrated pest management of coffee berry borer: strategies from Latin American that could be useful for coffee farmers in Hawaii. Insects. 7:3–24.*

*Baker, P. 1999. La broca del café en Colombia: informe final del proyecto MIP para el control de *Hypothenemus hampei*. CABI Bioscience, Ascot, United Kingdom. 118.*

*Barrera, J. F., A. Castillo, F. Infante, J. Gómez, and W. De La Rosa. 1989. Biología de *C. stephanoderis* (Betrem) (Hymenoptera: Bethylidae) en laboratorio. Cicle biològic, capacitat de oviposició, i emergència del fruit del cafellat. Café Cacao, The Francia. 33: 101–108.*

*Benassi, V. L. 1995. Levantamiento dos inminuos naturais da broca do café *Hypothenemus hampei* (Coleoptera: Scolytidae) no norte do Espírito Santo. An. Soc. Entomol. 24: 635–638.*

*Bustillo, A., J. Orozco, P. Benavides, and M. Portilla. 1996. Producción masiva y uso de parasitoides para el control de la broca del café en Colombia. Rev. Col. Entomol. 47: 215–230.*

*Carey, J. R. 1993. Applied demography for biologist with special emphasis on insects. Oxford University Press, Oxford, United Kingdom. p. 206.*

*Carey, J. R., T. Y. Wong, and M. M. Ramadan. 1988. Demographic framework for parasitoid mass rearing: case study of *Biosteres tryony* (Hymenoptera: Braconidae), a larval parasitoid of tephritid fruit flies. Theor. Popul. Biol. 34: 279–296.*

*Hargreaves, H. 1926. Notes on the Coffee berry bore. Bull. Entomol. Res. 16: 347–354.*

*Hargreaves, H., 1935. *Stephanosidea hampei* Ferr. Coffee berry borer in Uganda. East Afr. Agric. 1:218–224.*

*Infante, F. and L. J. Barrera. 1993. Estadísticos demográficos de *Cephalonomia stephanoderis* Betrem (Hymenoptera: Bethylidae) a temperaturas constantes. Folia. Entomol. Mex. 87: 61–72.*

*Infante, L. J. Barrera, J. Gomez, and A. Castillo. 1992. Thermal constants for pre-marginal development of the parasitoid *Cephalonomia stephanoderis* Betrem (Hymenoptera: Bethylidae). Can. Ent. 124: 935–941.*

*Infante, F., J. Valdes, V. Penagos, and J. Barrera. 1994. Description of the life stages of *Cephalonomia stephanoderis* (Hymenoptera: Bethylidae), a parasitoid of *Hypothenemus hampei* (Coleoptera: Scolytidae). Vedala. 1: 13–18.*

*Jervis, M. A. and M. J. Copland. 1996. The life cycle. In: M. A. Jervis and N. Kidd (ed.), Insect natural enemies. Chapman and Hall, London. pp. 63–161.*

*Krebs, C. J. 2001. Ecology: the experimental analysis of distribution and abundance, 5th ed. Wesley Longman, San Francisco, CA. p. 695.*

*Kock, V. J. 1973. Abondance de *Hypothenemus hampei* Ferr. Scolyte des graines de café en function de sa plante hote et de son parasite *Cephalonomia stephanoderis* Betrem en Cote de’ Ivore. Medd. Landbou. 73: 1–85.*

*Murphy, S. and D. Moore. 1990. Biological control of the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae): previous programs and possibilities for the future. Biol. Control. 11: 107–117.*

*Murphy, S. T. and D. K. Rangi. 1991. The use of the African wasp, *Prorops nasuta* for the control of the Coffee Berry Borer, *Hypothenemus hampei* in Mexico and Ecuador: the Introduction program. Insect. Sci. Applic. 12: 27–34.*

*Portilla, M. 1999a. Mass rearing technique for *Cephalonomia stephanoderis* (Hymenoptera: Bethylidae) on *Hypothenemus hampei* (Coleoptera: Scolytidae) developed using Cenibroca artificial diet. Rev. Col. Entomol. 25: 57–66.*

*Portilla, M. 1999b. Desarrollo y evaluación de una dieta artificial para la cria masiva de *Hypothenemus hampei* (Coleoptera: Scolytidae). Rev. Col. Entomol. 1: 24–38.*

*Portilla, M. 1999c. Mass production of *Cephalonomia stephanoderis* on *Hypothenemus hampei* reared using artificial diet. Thesis. University of London, England. 253 pp.*

*Portilla, M. and A. Bustillo. 1995. Nuevas investigaciones en la cria masiva de *Hypothenemus hampei* y de sus parasitoides *Cephalonomia stephanoderis* y *Prorops nasuta*. Rev. Col. Entomol. 21: 25–33.*

*Portilla, M. and D. Streit. 2006. Nuevas técnicas de producción masiva de *Hypothenemus hampei* sobre la dieta artificial Cenibroca modificada. Rev. Col. Entomol. 57: 37–50.*
Portilla, M. and D. Streett. 2008. Avances investigativos en la producción masiva automatizada de la broca del café Hypothenemus hampei (Coleoptera: Scolytidae) y de sus parasitoides sobre dietas artificiales. Sis. Agroeco. Mod. Biomatematics. 1:9–12

Portilla, M., J. Ramos-Morales, G. Rojas, and C. Blanco. 2014. Life tables as tools of evaluation and quality control for arthropods mas production. In: J. Morales-Ramos (ed.) Mass production of beneficial organisms, pp. 241–275. Academic Press, New York. 742 pp.

Pressat, R. 1985. The dictionary of demography. Bell and Bain, Ltd., Glasgow. Puzzi, D. 1939. Valor du parasitismo da Prorops nasuta Waterson no cambate a brocada cafe. J. Agrono. 2: 259–264.

Quintero, C., A. E. Bustillo, P. Benavides, and B. Chavez. 1998. Evidencia del establecimiento de Cephalonomia stephanoderis y Prorops nasuta (Hymenoptera: Bethylidae) en cafetales del departamento de Nariño, Colombia. Rev. Colomb. Entomol. 24:141–147.

Ruiz-Cardenas, R. and P. Baker. 2010. Life table of Hypothenemus hampei (Ferrari) in relation to coffee berry phenology under Colombian field conditions. Sci. Agric. 67: 658–668.

Salazar, H. M. and P. Baker. 2002. Impacto de liberaciones de Cephalonomia stephanoderis sobre poblaciones de Hypothenemus hampei. Rev. Col. Entomol. 53: 306–316.

SAS Institute. 2013. SAS/STAT user’s manual, version 9, 4th ed. SAS Institute, Cary, NC.

Shaw, M. 1994. Parasitoid host range. In: B.A. Hanwkins and W. Sheeham (eds.). Parasitoid community ecology, Oxford University Press, Oxford, United Kingdom, pp. 11–144.

Ticheler, J. H. 1961. Etude analytique de l’ épidemiologie du scolyte des graines de café Stephanoderis hampei Ferr., en Côte d’ Ivoire. Medde. Landh. 61: 1–49.

Toledo, A. A. 1942. Notas sobre a biologia da vespa de Uganda, Prorops nasuta Waterson, (Hymenopera: Bethylidae) no estado de S. Paulo–Brasil. Arqu. Inst. Biol. 13: 233–260.

Vijayalakshmi, C. K., C. Simi, K. Tintumol, and P. K. Vinodkumar. 2014. Life cycle of the coffee berry borer parasitoid, Cephalonomia stephanoderis (Hymenoptera: Bethylidae) on parchment and cherry coffee. Int. J. of Sci. Tech. Research. 3: 151–152.