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Impact of Multiple Infestations by Colonizing Coffee Berry Borer, *Hypothenemus hampei*

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ABSTRACT

The coffee berry borer, *Hypothenemus hampei* (Ferrari) is the most devastating pest of coffee worldwide. *Hypothenemus hampei* has cryptic biology, i.e. the borer spends its entire life cycle inside the coffee berry. Multiple infestations of *H. hampei* in a single berry is a rare event. However, due to the heterogeneous flowering pattern and difference in the phenology, a range of coffee berry stages are always available for infestations. Additionally, multiple infestations in leftover/non-harvested berries are common in offseason. The multiple infested berries establish a limiting resource among conspecifics of *H. hampei*. Results of the study indicated a positive correlation between progeny and coffee berry weight. However, the crowding of conspecifics resulted in the reduction of the progeny numbers. The decrease in multiple infested berries and behaviour of colonizing females during cohabitation are discussed.

Key words: Coffee, Multiple infestations, Crowding, Colonizing female, Cohabitation

The coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae), is recognized as a major threat to coffee production worldwide (Damon 2000, Jaramillo *et al.* 2006). *Hypothenemus hampei* colonization behaviour has been a subject of debate. Several studies have reported that *H. hampei* uses marking pheromone because of which multiple infestations are assumed as a rare event unless there is a scarcity of coffee berries (Jaramillo *et al.* 2013, Njihia *et al.* 2014). In general, there is usually one infestation per berry. However, during severe infestations, more than one adult bore into a single berry with its entrance (Wrigley 1988, Vega *et al.* 2015). During the inter-harvest period, the adult population can level up to 150 adults per berry and reproduction continues until the exhaustion of resources (Baker 1984).

Because of heterogeneous flowering pattern and fruiting between *Coffea arabica* L. and *C. canephora* Pierre ex A. Froehner, a range of coffee berry stages are always available for infestations (Baker and Barrera 1993). Hence, multiple infestations in leftover/unharvested berries are common in a season as well as during offseason. Coffee berries present during the off-season are reservoirs for *H. hampei* (Johnson *et al.* 2019). Thus crowding of colonizing females is unavoidable because of the limited resource. A study on such resource partitioning helps to understand how the conspecific females can coexist in the same niche for survival and the impact of differential use of the resource. As *H. hampei* is a synovigenic species (Silva *et al.* 2012), feeding of coffee endosperm by colonizing females becomes critical for egg production. These nulliparous females are strongly attracted to volatile chemicals emitted by mature coffee berries, where adult females bore through a region identified as the disc (style remnant), and eggs are laid after excavating irregular galleries in the endosperm of the coffee fruit. Colonizing females do not abandon the original infested coffee berry and oviposition continue for 30 – 35 days (Roman-Ruiz *et al.* 2017a, 2017b, Alba-Alejandre *et al.* 2018).

Although competition in phytophagous insects is an unusual event, several studies on scolytid beetles have

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identified competition for food and breeding sites (Schlyter and Anderbrant 1993). Thus multiple infested berries in case of *H. hampei* establish a limiting resource for oviposition and development of offspring. Fluctuations in food availability affect the activity patterns of residents and can result in competition between colonizing females. Besides, food is very critical for colonizing females since that decides the probability of extended survival during the inter-harvest season. It is difficult to interpret individual behaviours without establishing a limiting factor as one population/ an individual can significantly lower the level of limiting resource available to other individuals. Thus, it is essential to identify whether colonization and development of offspring of *H. hampei* could be better if they were alone or with the presence of other females. Therefore, the present study was carried out to know whether food is a potentially limiting resource for the development of *H. hampei* in the varied size of coffee berries in multiple infestations.

MATERIALS AND METHODS

Collection: Initial field surveys were conducted for assessing the *H. hampei* population in the Chikkamagaluru region, Karnataka, India at a private plantation (13°26'41.4"N 075°48'29.5"E, 1067m elevation) with severe *H. hampei* infestation for the collection of infested coffee berries. Infested coffee berries were identified based on the presence of the borer entrance pinhole with powdery substance indicating active tunnelling and feeding within the berries. Coffee berries with signs of *Beauveria bassiana* infection were excluded.

Weight of coffee berries: Harvested coffee berries were weighed individually and sorted into several groups according to the weight of the infested fruits and number of entrance holes. At the end of the experiment, the weight of the coffee berries was retaken, and the final weight was substituted with initial weight to quantify the food resource used by the colony of *H. hampei*. The difference between two weights of the berries was considered for the measurement of consumed food.

Culture maintenance in the laboratory: Coffee berries were surface sterilized with 2% sodium hypochlorite solution and were maintained individually according to the weight and number of entrance holes. The labelled test tubes (8.5 cm height × 2cm diameter) containing individual berries were covered with cotton plugs to prevent the escape of emerging *H. hampei* beetles. Bottom of the test tubes was filled with plaster of Paris and charcoal for holding moisture. Distilled water was added regularly to avoid the desiccation of the coffee berries. Test tubes containing infested berries were maintained in the growth chamber (GC-300TLH, Jeiotech, Korea) at temperature 25±1°C and humidity 70±5% RH as followed by Jaramillo *et al.* (2009). Although several berries with more than three entrance holes were found during the field collections, the study was limited to berries maximum of three infestations per berry due to the lack of coffee berries with constant weights.

Analysis

Colonizing *H. hampei* females which emerged naturally in search of fresh berries were counted. Coffee berries were destructively sampled after 100 days using disposable blade under stereo zoom microscope (Lawrence and Mayo, Trinocular Research Microscope) to find the number of adults inside the berries. Contents of the berry after dissection were transferred to a Petri dish layered with filter paper and adults found inside were separated from the frass and other debris. No distinction was made in the count between male and female as *H. hampei* has the female-biased adult sex ratio of 1Male:10 Females (Jaramillo *et al.* 2009). Developmental stages, i.e. egg, larvae, and pupae present in the berries were also counted. Infested berries with less than five number of individuals were considered as incomplete infestations and were not considered in the study. Coffee berries colonized by Coffee bean weevil, *Araecerus fasciculatus* (DeGeer) (Coleoptera: Anthribidae) identified by emergence holes (3mm diam) were also excluded. Results of the experiments were subjected to regression analysis.

RESULTS AND DISCUSSION

Results indicated a positive correlation between the average number of adults developed and coffee berry weight (Fig 1). There was an intrinsic rate of population increase irrespective of the number of infestations with the increasing weight of coffee berries. The value of the coefficient of determination (R^2) of one, two, and three females was 0.78, 0.64 and 0.71. The values indicated that 78, 64 and 71% of the variability among the dependent variables in the model explainable by the independent variable.

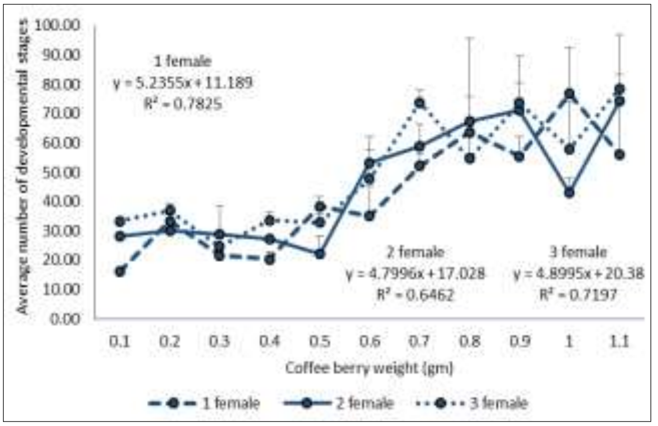

Fig 1 Distribution of the average number of developmental stages and coffee berry weight per fruit in one, two, and three female infested coffee berry. Data are Mean ± SE

Some volatiles secreted by coffee berries is known to regulate infestation of colonizing females. Three spiroacetals, i.e. conophthorin, frontalin and brocain regulate chemical ecology of colonizing *H. hampei* females to discriminate infested berries to avoid competition. Thus it repels the other colonizing females approaching for the same niche (Njihia *et al.* 2014). However, when the choice of niche reduced, colonizing females may be forced to share/occupy the same niche irrespective of semiochemicals, especially in leftover berries during offseason. Thus colonizing females exhibit distinctive behavioural pattern under varying conditions. A range of developing coffee berries always available for infestations due to the heterogeneous flowering pattern of *C. arabica* and *C. canephora;* coffee ripening occurs earlier in *C. arabica* than that of *C. canephora*. Thus a range of coffee berry stages is always present for infestations by *H. hampei* (Baker and Barrera 1993, Bal *et al.* 2011).

Apart from *C. arabica* and *C. canephora*, several species of tree coffee are also grown in the borders of the plantations in India. Coffee berries from these trees end up un-harvested due to late-ripening and difficulty in harvesting from big trees. Thus un-harvested berries on these trees are also considered as a niche for *H. hampei* colonizing females (Balakrishnan *et al.* 2013). Further, during the dry period colonizing females co-occur in leftover berries where they share one shelter due to the shortage of berries. Dry berries during this period form a substantial reservoir for subsequent infestations by *H. hampei* females (Mathieu *et al.* 1997). Thus carrying capacity of the berry niche determines their size, reproductive potential and longevity of the adult borer to survive from one coffee season to the next. *Hypothenemus hampei* is a synovigenic species and feeding on coffee endosperm is critical for egg production (Silva *et al.* 2012). In many cases, competition among individuals does not take place directly. Instead, individuals respond to the decrease in the level of a resource by the activity of other individuals. Thereby they limit the growth and reproductive success of other individuals. This type of competition is referred to as 'exploitation'. In interference type of competition, where individuals respond directly by preventing others from exploiting resources. In number instances, elements of both exploitation and interference can be observed. For example in *Neapheanops tellkampfi* (Coleoptera: Carabidae), adult beetles compete among each other for feeding on cricket eggs, where beetles fecundity is directly correlated with cricket fecundity (Griffith and Poulson 1993, Begon *et al.* 2006).

Hypothenemus hampei is identified as a cryptic insect due to its biology. The multivoltine *H. hampei*, with overlapping developmental stages, spends most of its life cycle hidden inside the coffee berry. They are thus making it challenging to observe the behaviour/activity patterns. The founder females oviposit in clutches close to the seed periphery and continue to make tunnels in the endosperm towards the centre of the berry to spread the progeny to reduce competition (Alba-Alejandre *et al.* 2018). The egg-laying continues for 30-35 days, where founder female continues to make tunnels further while covering most of the area/space of coffee berry (Roman-Ruiz *et al.* 2017b). Upon hatching, emerging larva consume the seed. Thus, resulting in depletion of resource makes it difficult for other colonizing females to utilize the resource.

Our study showed that progeny of the infesting colonizing *H. hampei* females increased with the increase in food resource. However, in the case of berries colonized by two or three females, the number of progeny did not reach the expected 2-3 fold increase. Reason for the reduced progeny could be due to the sharing of limited resource between the conspecifics. Another possibility is marking pheromone produced by the colonizing females responsible for reduced fecundity reported in other insects as a strategy to compel conspecifics (Njihia *et al.* 2014, Vega *et al.* 2011). Additionally, according to Baker *et al.* (1992, 1994), colonizing *H. hampei* females remove dead immature stages from the berry for brood hygiene and thus making it difficult to document the possible competition.

In insects at higher population density, competition among individuals for food and mate leads to low fecundity (Flanagan *et al.* 1998, Varley *et al.* 1974). Reduced fecundity of colonizing *H. hampei* females in the presence of competitors was due to the crowding of 2-6 females per berry, which reduced the borer fecundity (Njihia *et al.* 2014). A similar observation was reported by Vega *et al.* (2011) in artificial diet, where increasing the female density from one to five did not result in expected folds of increase in the progeny despite to food resource availability.

Cannibalism in *H. hampei* was ambiguous until recently. Vega *et al.* (2017) observed a *H. hampei* female eating eggs and biting the larvae resulting in the formation of a necrotic area. In an experiment when *H. hampei* females were cohabitated in an artificial diet, where individual colonizing females were observed to attack/push other females (Kiran and Venkatesha 2016). Similar observations have been recorded by Borsa and Kjellberg (1996), where competition among females in artificial diet led to fighting, occasional mutilation, which resulted in changes in brood sex ratio.

In our study in a few berries, several live larvae and pupae were found outside the berries. Similar observations have been made by Baker *et al.* (1994) at higher humidities, where the author reported that there might be some form of control by founder colonizing females. The author concludes this sort of the nest cleaning carried for brood hygiene by colonizing females.

Our study indicates that the cohabitation of conspecific females in a single berry establish a limiting resource among conspecifics. Although the results of the study indicated a positive correlation between progeny and coffee berry weight, the change in progeny number did not reach the expected 2-3 (multiple) fold increase. Our observation attributes the discrepancy of control to adequate resources to the borer progeny to complete the life cycle.

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