Development and behavioral ecology of *Conopomorpha cramerella* (Lepidoptera: Gracillariidae)

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Abstract

Conopomorpha cramerella (Snellen) (Lepidoptera: Gracillariidae) is the most devastating pest responsible for the decline of cocoa (cacao) production in Southeast Asia in the last few decades. Despite its economic importance, the basic ecological knowledge of the pest is poorly understood, indirectly resulting in poor efficacy of current pest management methods. Our study confirmed and updated the *C. cramerella* life cycle, and measured the natural distribution within trees in managed cocoa orchards, and movement of adults after they were disturbed. These nocturnal moths rest beneath branches during the d, with a strong preference for nearly horizontal branches. Females demonstrated a greater capacity for movement after disturbance compared to males (83.0 ± 89.9 cm in 9.1 ± 9.5 s versus 57.7 ± 49.2 cm in 6.7 ± 5.3 s for females and males, respectively), and rest closer to cocoa pods (61.0 ± 45.0 versus 76.0 ± 47.3 cm for females and males, respectively). Our observations described herein bring new ecological knowledge and provide new perspectives on potential IPM methods for pest *C. cramerella* populations.

Key Words: *Theobroma cacao*; cocoa pod borer; distribution; resting sites

Resumen

Conopomorpha cramerella (Snellen) (Lepidoptera: Gracillariidae) es la plaga más devastadora responsable del declive de la producción de cacao en el sudeste asiático en las últimas décadas. A pesar de su importancia económica, el conocimiento ecológico básico de la plaga es poco conocido, lo que resulta indirectamente en una mala eficacia de los métodos actuales de manejo de plagas. Nuestro estudio confirmó y actualizó el ciclo de vida de *C. cramerella*, midió la distribución natural dentro de los árboles en huertos de cacao manejados y el movimiento de adultos después de que fueron perturbados. Estas polillas nocturnas descansan debajo de las ramas durante el dia, con una fuerte preferencia por las ramas casi horizontales. Las hembras demostraron una mayor capacidad de movimiento después de la perturbación en comparación con los machos (83.0 ± 89.9 cm en 9.1 ± 9.5 s versus 57.7 ± 49.2 cm en 6.7 ± 5.3 s para hembras y machos, respectivamente) y descansan más cerca de las vainas de cacao (61.0 ± 45.0 versus 76.0 ± 47.3 cm para las hembras y los machos, respectivamente). Nuestras observaciones descritas aquí aportan nuevos conocimientos ecológicos y brindan nuevas perspectivas sobre los métodos de MIP potenciales para las poblaciones de *C. cramerella*.

Palabras Clave: *Theobroma cacao*; barrenador de vainas de cacao; distribución; sitios de descanso

Cocoa (cacao) (*Theobroma cacao* L.; Malvaceae) is a major crop in the economy of the Southeast Asia archipelagos. It was brought from Latin America to the Philippines by the Spaniards during the 16th century (Day 1985), and was then introduced into Indonesia on Sulawesi Island in the mid-17th century (Toxopeus & Weisberger 1983; Durand 1995). In 2016, Indonesia was ranked third among the cocoa producing countries worldwide after The Republic of Côte d'Ivoire and Ghana (McMahon et al. 2015; FAO 2018). *Conopomorpha cramerella* (Snellen) (Lepidoptera: Gracillariidae) was first described as a pest at the beginning of the 20th century, but earlier reports of damage were noted by Jansen (1860). *Conopomorpha cramerella* is an endemic species of the Southeast Asia and western Pacific archipelagos (Malaysia, Philippines, Indonesia) (De Prins & De Prins 2005). It is thought that the first appearance of *C. cramerella* in Indonesia occurred in North Sulawesi in the mid-1800s. After a rapid decline in Sulawesi Island, cocoa production was expanded in Java and in the Philippines in the 1880s as an alternative to coffee. *Conopomorpha cramerella* was suspected to have been introduced into Sabah, East Malaysia, during the 1980s, most likely from infested pods brought from Indonesia or the Philippines, followed by similar introductions in West Malaysia. The most recent known introduction is considered to be in Papua New Guinea about a decade ago. Along with multiple introduction events of the pest, it is hypothesized that there was a host switch from the native Sapindale hosts like rambutan (*Nephelium lappaceum* L.; Sapindaceae) and langsat (*Lansium parasiticum* (Osbeck) Sahni & Bennet; Meliaceae) to cocoa (Azhar & Long 1996; Posada & Vega 2005). Since then, the distribution of *C. cramerella* and the level of damage to cocoa production have both increased exponentially. Today *C. cramerella* is one of the most devastating pests of cocoa in Southeast Asia. This pest is currently responsible for an average of 40 to 60% loss of cocoa production, and up to 80 to 90% losses in unmanaged farms. This is worth about USD $500 million annually for the Indonesian cocoa industry alone, and was responsible for the drastic reduction of the cocoa industry in Malaysia (ICCO 2015).

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The adult is a small nocturnal moth about 7 mm in length, easily recognized by its long antennae that fold back above the wings when at rest, and commonly perches on the underside of host branches during the day (Day 1985; Day et al. 1994). At dusk, gravid females take flight and seek out cocoa pods, laying their eggs directly on the outer husk. Within 3 d, the eggs hatch and larvae exit through the bottom of the egg and tunnel through the pod epicarp, mesocarp, and endocarp, eventually feeding on the pulp and placenta surrounding the beans. Destruction of the placenta disrupts normal development of the beans, resulting in bean size and fat content reduction, and callus-forming reaction resulting in bean clumping. Beans from highly infested pods usually are not extractable from the pod, and cannot be used for processing and chocolate production. With light infestations, losses are typically not significant; however, control still may be warranted to prevent development of high pest populations.

Several control methods have been implemented to reduce the impact of *C. cramerella*. Sleeving cocoa pods with plastic sleeves that prevent females from ovipositing has been shown to be the most effective control method, but is very labor intensive (Youdeowei 1980; Vanialingam et al. 1981). Biological control efforts using black ants (See & Khoo 1996), parasitoids (Vos et al. 2003), or entomopathogens (Rosmana et al. 2009) did not provide effective results or were not economically feasible (Lim & Pan 1986). Complete harvesting of the cocoa pods in order to break the life cycle of the moth achieved only temporary population reduction, as *C. cramerella* could be reintroduced easily from locations where farmers did not follow recommendations, or from populations breeding on alternate hosts (Lim 1992). Weekly harvesting of all ripe pods is an effective way of controlling *C. cramerella*, but considered highly time and labor intensive by the farms. At present, an effective method for control remains the use of pesticides (Wood et al. 1992; Beevor et al. 1993; Teh et al. 2006), but the cost/efficiency ratio remains poor due to the cryptic behavior of the insect (i.e., the larval stages are protected within the pod and not exposed to topical insecticides) (Chang 2013).

Surprisingly, the development and behavioral ecology of this major pest is still poorly understood, and this lack of knowledge is likely an underlying reason for the failure of most integrated pest management (IPM) programs for *C. cramerella*. A better understanding of the biology and behavior of this insect is an essential foundation for both basic and applied research necessary to develop effective methods of pest control and mitigate the impact of *C. cramerella* in cacao orchards. The objectives of the current study were (1) to confirm and update some of the biological and ecological knowledge regarding the life cycle, (2) to highlight the natural distribution of the adults in managed cocoa orchards, and (3) to quantify the flight distance and duration after a disturbance.

Materials and Methods

INSECT COLLECTIONS AND REARING

Cocoa pods showing premature yellowing of the husk, a characteristic symptom of *C. cramerella* infestation (Beevor et al. 1986), were collected in the field and placed on a layer of dried cocoa leaves in bugdorms sized 61 × 61 × 61 cm (Bioquip Inc., Rancho Dominguez, California, USA) under both laboratory conditions (27–31 °C, 60–70% RH) and outdoor condition (28–33 °C, 70–90% RH). The last larval instars exit the pods to spin their cocoons among the dried leaves for pupation. Leaves were checked daily, and cocoons collected and placed in mesh cages for adult emergence. Newly emerged adults were collected, sexed, and placed with adults of the same age and gender. Moths were provided with honey solution (10%) and the duration of the adult stage was recorded. Additional adults captured directly from the field also were kept in mesh cages under laboratory conditions, as well as in outdoor conditions described above. An unripe cocoa pod, 10 to 12 cm long, was provided overnight as an oviposition substrate. Eggs laid on the pod were monitored daily to measure the egg stage duration and hatching success.

SEXING INDIVIDUALS

Examination of external genitalia was used to determine the sex of live adults captured in the field or emerging from pupae in the laboratory, as described in Bradley (1986). The hairy anal papillae of the ovipositor characterized the female genitalia, whereas males were confirmed by a darker and wider caudal segment and the presence of a hair pencil. Observations were done using a camera (5MP camera MU500-PB10, Amscope, Irvine, California) mounted on an Amscope 3.5X-0.90X Track Stand Stereo Zoom binocular microscope (Amscope, Irvine, California).

FIELD LOCATION AND PEST DISTRIBUTION

Field captures of adults were conducted from Nov 2015 to Nov 2017 in 3 small cacao farms located in Angkona, South Sulawesi, Indonesia (2.562800°S; 120.936000°E). In each farm, cocoa trees were planted 3 m apart within a row, with 3 m spacing between rows. No shade trees were present in these cocoa fields. About 100 trees were carefully inspected between 10:00 AM and 12:00 PM to collect adults at rest. Once a moth was located on a branch, it was hand-captured alive using a cylindrical plastic bag (Zebra® Super Cemelang, Jakarta, Indonesia) measuring 1.5 cm diam × 10 cm long and sexed. The resting site was described using the following parameters: height, distance from the trunk, distance from the nearest available cocoa pod older than 2 mo or more than 8 cm long (i.e., susceptible to infestation), branch diam at the resting site, and angle of the branch compared to horizontal. In addition, the temperature at the resting site (underside of branch) and on the branch surface above the resting site was measured using an infrared laser portable thermometer (Raytek Raynger St®, Wilmington, North Carolina, USA). Twenty branches exposed to sunlight and others shaded by the canopy were selected for these measurements.

FLIGHT DISTANCE AND DURATION AFTER DISTURBANCE

When at rest, adult moths often are disturbed naturally by wind, rain drops, or other insects moving along the branches (potential antagonistic interspecific interactions). When such a disturbance occurs, the moths usually fly away from the disturbance to locate a new resting site on either the same or a different branch on the same tree, or on another tree nearby. In this experiment, branches used as resting sites were briefly shaken to create a disturbance that would initiate flight. The duration of flight and distance between take-off and landing sites were measured. Once the individual landed, it was captured, sexed, and brought to the laboratory.

STATISTICAL ANALYSIS

Student *t*-tests were used to determine differences in sex ratio between field and laboratory conditions (N = 166 and 45, respectively): differences between the sexes in duration of the pupal stage (N = 22 and 18 for females and males, respectively), in the adult distribution in the field for distance from the first pod, distance from trunk, branch diameter at the resting sites and height of the resting sites (N = 217 and 372 for females and males, respectively), in flight distance and flight duration after disturbance (N = 43 and 85 for females and males, respectively), and also differences in temperature between shade- and light-exposed branches (N = 10 for both light exposures). Changes in sex ratio over time was analyzed using the Kruskall-Wallis test (Statistica12®, Dell Inc., Tulsa, Oklahoma, USA). Results are reported as mean ± SD unless otherwise indicated.

Results

PEST LIFE CYCLE

Duration of the egg stage was 3.2 ± 0.2 d and 3.1 ± 0.2 d under field and laboratory conditions, respectively (t = 1.283; df = 64; P = 0.205). Sex did not affect duration of the pupal stage (t = 1.084; df = 102; P = 0.280) or adult life span (t = 0.010; df = 38; P = 0.921). Therefore, when pooled over both sexes, duration of pupal stage was 8.2 ± 0.8 d, and adult lifespan was 6.1 ± 2.0 d. Successful adult emergence was obtained from 66.2 ± 15.5% of the pupae collected.

SEX RATIO

The adult sex ratio at emergence was 1:1, with no difference between indoor and outdoor conditions (t = 0.404; df = 86; P = 0.687, N = 2464). However, the sex ratio at emergence varied significantly from that observed in the adult population captured in the field (t = -5.577; df = 209; P = 0.00001). The latter sex ratio showed a bias toward males (1.2♂:0.8♀) (t = 15.452; df = 330; P = 0.001) and did not vary over time (H [11, N = 166] = 14.623; P = 0.2004).

ADULT DISTRIBUTION

Adults were caught resting on the underside of the branches, but not on the trunk or leaves. Adults observed in flight for a few s before landing on a branch quickly walked to the underside of the branch. When a flying individual was observed landing on a leaf, it took off immediately to find another resting site underneath a branch. Resting adults usually were positioned perpendicularly to the branch. No differences between sexes were observed in the branch diameter used as resting sites (t = 1.072; df = 522; P < 0.0001) or in the distance from the trunk (t = 0.882; df = 587; P = 0.109). However, females were found resting significantly closer to the nearest susceptible pods (t = −3.797; df = 587; P = 0.0002) and higher in the tree canopy than males (t = −3.807; df = 587; P = 0.0002) (Fig. 1).

Most farmers in Angkona (South Sulawesi, Indonesia) prune their cocoa trees into a ‘cup shape,’ removing horizontal branches and branches with lower angles, and keeping the higher angle branches that point upward (Table 1). Consequently, the number of branches available as resting sites was biased toward high angled branches (88% of available branches are ≥ 45°). When the relative availability of branches was taken into account, branches with lower angles were significantly favored as *C. cramerella* resting sites, with the highest preference for horizontal branches (χ^2 = 80.92; df = 4; P < 0.0001) (Table 1).

TEMPERATURE AT THE RESTING SITES

The temperature at resting sites (underneath the branches) was 30.8 ± 2.8 °C, which was significantly lower than the temperature observed on the branch surface exposed to sunlight directly above the resting site (35.7 ± 3.9 °C) (t = 4.586; df = 38; P = 0.00005). No differences were observed between temperature at the resting sites (28.4 ± 2.4 °C) and on the branch surface directly above the resting site under shaded conditions (28.7 ± 2.5 °C; t = 0.283; df = 22; P = 0.779).

FLIGHT DURING DISTURBANCE

When disturbed, females tended to fly for a longer time period (t = 1.821; df = 126; P = 0.042) and travel a significantly longer distance (t = 2.051; df = 126; P = 0.042) than males (Fig. 2). The maximum distance recorded after disturbance was 5 m for females and 2.5 m for males.

Discussion

Despite the important socio-economic impact of *C. cramerella* in the Southeast Asia region, the limited knowledge of the ecology and behavior of this insect has been a constraint to finding suitable methods for pest control. Day (1985) has been and still is the primary source of ecological information on *C. cramerella*. Surprisingly few publications have covered the biology of this pest (Lim et al. 1982; Beevor et al. 1986; Lim 1992), especially when compared to the number of more recent studies directed at its sibling species *Conopomorpha sinensis* Bradley (Gracillariidae), which affects production of lychee (*Litchi sinensis* [Sonner.] J.F.Gmel.; Sapindaceae) in China (Schulte et al. 2007; Li et al. 2013; Meng et al. 2014; Fu et al. 2016; Zhang et al. 2016). Our observations described here bring new ecological knowledge, providing new perspectives on potential IPM methods for pest *C. cramerella* populations.

At emergence, the sex ratio in both laboratory- and outdoor-reared *C. cramerella* was 1:1, significantly different than the male-biased sex ratio observed in the field. No differences were observed in terms of adult lifespan between sexes, and there is no evidence that females are subject to higher predation under natural conditions. Females laying their eggs directly on the surface of the cocoa pods from dusk to dawn are in constant motion, displaying a characteristic host-seeking behavior with the abdomen curved downward to identify a favorable oviposition site (Day 1985). Laying an egg takes only a few s before the female resumes its oviposition seeking behavior. Predatory rate is expected to be low during this adult phase.

During the day, *C. cramerella* adults rest beneath the cocoa branches (Day 1985; Day et al. 1994). Both males and females share the same trees and co-occur on the same branches, usually perpendicular to branch orientation. In managed cacao orchards, trees are usually pruned ‘cup shape,’ presenting a higher proportion of high angled branches (88% are ≥ 45°). Both genders show a preference for resting sites on branches with angles less than 45° from horizontal. Perching on the underside of near-horizontal branches provides better protection from other insects (because of their abundance, ants are an important factor of disturbance anywhere on the tree), and from rain drops, the 2 main causes of disturbance during the diurnal quiescent period (Niogret unpublished data).

Our main hypothesis for such preferences is that the moths are attracted by darker surfaces during the day, which are significantly cooler than the surface directly exposed to sunlight; near-horizontal branches would provide more shade during the hottest parts of the day compared to higher angled branches. Females also were found resting closer to the cocoa pods than the males. This would be adaptive for females, improving the likelihood of finding a suitable host fruit during the nocturnal host-seeking period. Further research is needed to determine if proximity to the pods is the result of visual cues, chemical cues, or a combination of the 2.

The distribution of resting males and females differed by height within a host tree. Females were found significantly higher in the canopy compared to males. This height preference could explain the differences in sex ratio observed between laboratory-reared and field-captured *C. cramerella*. Resting higher in the canopy, females are less visible and less likely to be caught. Our observation also corroborates a

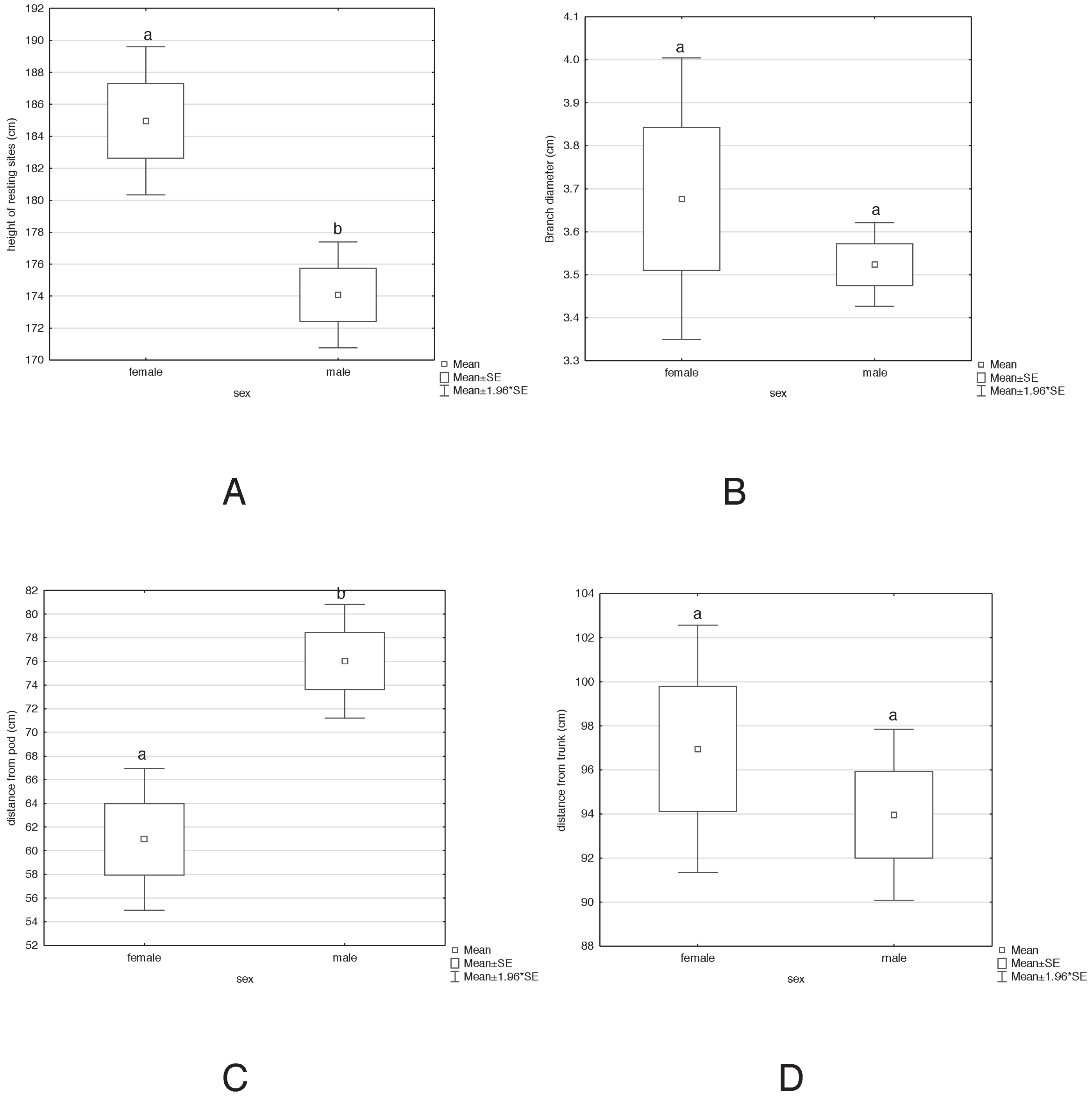

Fig. 1. Distribution of the adult *Conopomorpha cramerella* resting sites observed in the field related to (A) the height of the insect in the tree (cm), (B) the branch diameter (cm), (C) the distance from the nearest cocoa pod (cm), and (D) the distance from the trunk (cm). Boxes labeled with the same letter within a figure are not significantly different.

previous study showing that efficacy of *C. cramerella* pheromone lures varies depending on trap position within the canopy (Beevor et al. 1986). These authors reported that pheromone traps hung in the highest part of the cocoa canopy or above the canopy caught more males than traps hung at lower levels. It is likely that pheromone-emitting virgin females call from the uppermost portion of the tree, and males have evolved to respond to females at these higher calling sites.

At present, no information is available on the dispersal behavior and migratory capacity of *C. cramerella*. Lim et al. (1982) recorded an anecdotic 153 m flight by a male released in the middle of a football field, which may not represent the migratory capacity of *C. cramerella* within a cocoa orchard, especially in terms of wind exposure that most likely affects the flight distance on such a small insect. However, the flight patterns, duration, and distance have been recorded for *C. sinensis*. Zhang et al. (2016) reported that adult *C. sinensis* could fly for up to 30 s consecutively, traveling an average distance of 14 m. However, the majority of their marked and released males were caught at 5 m from the release point. In this paper, we looked at

Table 1. Distribution of adult *Conopomorpha cramerella* resting sites in cocoa trees affected by branch angle and branch availability in a pruned cocoa orchard in Angkona, South Sulawesi, Indonesia.

Branch angle (°)	Observed distribution of the resting sites (%)	Branch availability (%)	Normalized distribution of the resting sites (%)
0	14.6	3.7	52.0
22.5	18.2	8.7	27.2
45	49.6	50.4	19.8
67.5	17.3	31.0	7.3
90	0.3	6.3	0.7

the flight capacity of male and female *C. cramerella* adults when artificially disturbed during the day, mimicking natural disturbance events. We found a higher average dispersal capacity for female *C. cramerella* compare to males, with females flying up to 5 m, twice as far as their male counterparts. This distance is enough to move from 1 tree to another within a cacao orchard; the distance between trees was about 3 m. Additional studies are needed to determine if there is a difference between genders in their flight capacity during normal nocturnal activity.

Based on our observations that adult *C. cramerella* prefer to rest on branches ≤ 45°, and that higher numbers of *C. cramerella* rest on unpruned trees when surrounded by pruned trees (Ekayanti unpublished data), use of unpruned trees as a trap crop should be evaluated as an IPM tool for potential control of *C. cramerella*. For use as a trap crop, an attractive barrier crop is planted to provide protection of a main 'cash' crop from infestation. The trap crop can be a different plant species or variety that is more attractive to the pest than the primary crop. This strategy tends to be more effective for insects of intermediate mobility like *C. cramerella*, rather than those that are passively dispersed by wind (e.g., aphids), or those strong fliers that descend on a crop from higher elevations (Hokkanen 1991). For *C. cramerella* IPM, rows of pruned cocoa trees as the cash crop can be alternated with rows of unpruned cocoa trees with near-horizontal branches of the trap crop. Nocturnal activities, as well as diurnal disturbances during the resting periods should force the *C. cramerella* to migrate from less favorable pruned trees to more favorable resting sites provided by unpruned trees. Favoring localized application of insecticides on unpruned rows where the pest is concentrated, preferably toward the upper canopy where females aggregate, should greatly impact the pest population in the whole orchard, as well as reducing the losses on the cocoa pods carried by those unpruned trees. The technique may not necessarily eliminate the pest, but it can substantially reduce their populations and the economic impact on the main crop. This method has been demonstrated to successfully protect tomatoes from the corn earworm, *Heliothis zea* (Boddie) (Lepidoptera: Noctuidae), by using trap rows of corn in the US (Whitcomb 1960; Kennedy & Margolies 1985); and also to protect corn against the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae), by interplanting potatoes (Kennedy & Margolies 1985). The trap crop also can be a different growth stage of the main crop species, as long as it is more attractive to the pest. Examples of successful use of trap crop systems using the same species have been summarized by Hokkanen (1991).

In conclusion, this report documented that the life cycle of *C. cramerella*, from egg to newly emerged adult, takes approximately 4 wk under ambient environmental conditions in Sulawesi, Indonesia, confirming previous reports (Wardojo 1980; Vanialingam et al. 1981; Wessel-Riemens 1981). The sex ratio for *C. cramerella* is 1:1, with a mean lifespan of 6 d for adults of both sexes. These nocturnal moths rest during the d on the shaded, underside of host branches, with a strong preference for branches that are horizontal. As compared to males, female *C. cramerella* demonstrated a greater capacity for flight when disturbed, preferred higher resting sites, and roosted much closer to cocoa pods. The latter observation suggests that host visual or chemical cues are used by female *C. cramerella*, and warrant further investigation for development of female-targeted detection systems. Our observations also indicate that *C. cramerella* may be a good candidate for use of a trap crop for IPM, particularly if coupled with a good trapping system (using specific pheromone or kairomone attractants). By concentrating the pest population into the same trees, this approach would facilitate targeted control efforts, reducing pesticide use as well as the costs of labor, an economic advantage for the Indonesian cocoa farmers. Furthermore, this would reduce chemical residues at harvest, lessen environmental and safety concerns, reduce impact on natural enemies (e.g., predators and parasitoids), and pollinators, and delay development of pesticide resistance. Large scale and long-term field evaluations of trap crop IPM are needed to test the efficiency of this approach for suppression of *C. cramerella* populations in Indonesia.

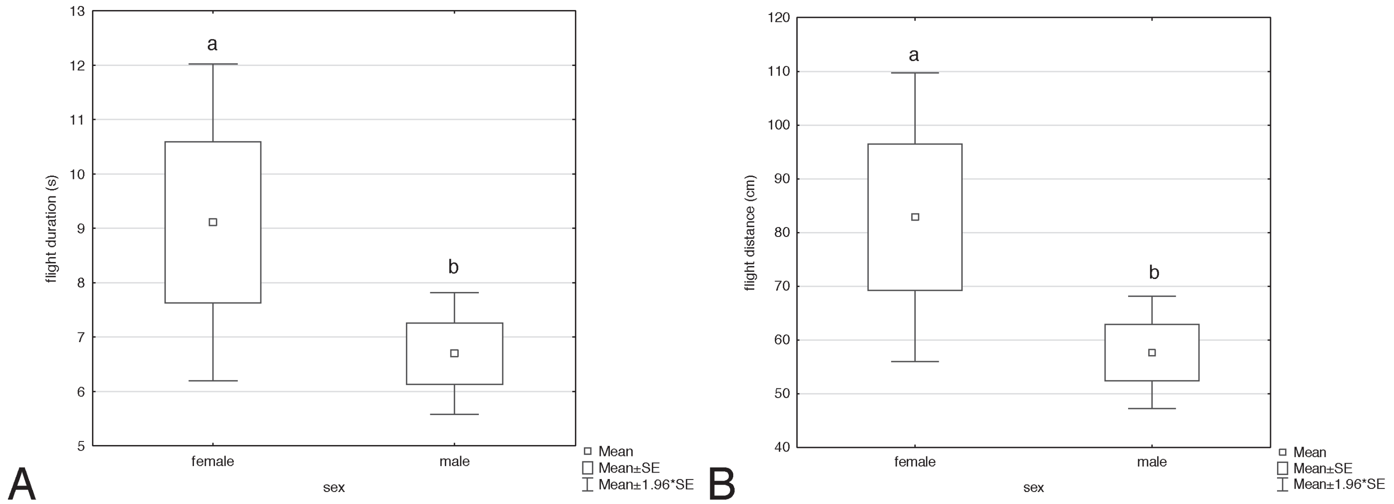

Fig. 2. Difference between the distance and duration of the flight between male and female *Conopomorpha cramerella* adults after disturbance during the diurnal resting period. Boxes labeled with the same letter within a figure are not significantly different.

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References Cited

Azhar I, Long GE. 1996. Effect of cocoa pod age on egg distribution and egg parasitism of the cocoa pod borer in Malaysia. Entomologia Experimentalis et Applicata 81: 81–89.

Beevor PS, Day RK, Mumford JD. 1986. Female sex pheromone of cocoa pod borer moth *Acrocercops cramerella*: identification and field evaluation, pp. 287–292 *In* Pushparajah E, Chew CP [eds.], Cocoa and Coconuts: Progress and Outlook. Incorporated Society of Planters, Kuala Lumpur, Malaysia.

Beevor PS, Mumford JD, Shah S, Day RK, Hall DR. 1993. Observations on pheromone-baited mass trapping for control of cocoa pod borer, *Conopomorpha cramerella*, in Sabah, East Malaysia. Crop Protection 12: 134–140.

Bradley JD. 1986. Identity of the South-East Asian cocoa moth *Conopomorpha cramerella* (Snellen) (Lepidoptera: Gracillariidae) with descriptions of three allied new species. Bulletin of Entomology Research 76: 41–51.

Chang ALS. 2013. The use of Wald's sequential probability ratio test (SPRT) in cocoa pod borer management. Jurnal Teknologi (Sciences & Engineering) 63: 5–10.

Day RK. 1985. Control of the cocoa pod borer (*Conopomorpha cramerella*). PhD Thesis, University of London, London, United Kingdom.

Day RK, Mumford JD, Hing HS. 1994. Adult resting sites as a target for chemical control of the cocoa pod borer *Conopomorpha cramerella* (Lepidoptera: Gracillariidae) in Malaysia. Bulletin of Entomological Research 85: 45–52.

De Prins W, De Prins J. 2005. Gracillariidae (Lepidoptera). World Catalogue of Insects 6: 1–502.

Durand F. 1995. Farmer strategies and agricultural development: the choice of cocoa in eastern Indonesia, pp. 315–338 *In* Ruf FAS, Siswoputranto PS [eds.], Cocoa Cycles: The Economics of Cocoa Supply. Woodhead Publishing Limited, Cambridge, United Kingdom.

FAO (Food and Agriculture Organization of the United Nations). 2018. (online) http://www.fao.org/faostat/en/#search/Cocoa%2C%20beans (last accessed 29 Jan 2019).

Fu H, Zhu FW, Deng YY, Weng OF, Hu MY, Zhang TZ. 2016. Development, reproduction and sexual competitiveness of *Conopomorpha sinensis* (Lepidoptera: Gracillariidae) gamma-irradiated as pupae and adults. Florida Entomologist 99: 66–73.

Hokkanen HMT. 1991. Trap cropping in pest management. Annual Review of Entomology 36: 119–138.

Jansen AJF. 1860. Aentekingen betreffende de kakao cultuur in de residentie Manado. Natuurkundig Tijdschrift voor Nederlendsch Indie 20 vierde serie deel VI: 289–307.

ICCO (International Cocoa Organization). 2015. Pest and diseases. Cocoa pod borer (*C. cramerella*). https://www.icco.org/about-cocoa/pest-a-diseases.html (last accessed 20 Jan 2019).

Kennedy GG, Margolies DC. 1985. Mobile arthropod pests: management in diversified agroecosystems. Bulletin of Entomological Society of America 31: 21–27.

Li P, Chen B, Dong Y, Xu S, Chen K. 2013. Effect of temperature and supplementary nutrition on the development, longevity and oviposition of *Conopomorpha sinensis* (Lepidoptera: Gracillariidae). Florida Entomologist 96: 338–343.

Lim GT. 1992. Biology, ecology and control of cocoa pod borer *Conopomorpha cramerella* (Snellen), pp. 85–100 *In* Keane PJ, Putter CAJ [eds.], Cocoa Pest and Disease Management in Southeast Asia and Australia. FAO Plant Production and Protection Paper No. 122. FAO, Rome, Italy.

Lim GT, Pan KY. 1986. Observations on the sexual activity and egg production of cocoa pod borer *Conopomorpha cramerella* (Snellen) in the laboratory. Annual Research Report, Department of Agriculture, Kota Kinabalu, Sabah, Malaysia.

Lim GT, Tay EB, Pang TC, Pan KY. 1982. The biology of cocoa pod borer *Acrocercops cramerella* Snellen and its control in Sabah, Malaysia, pp. 257–287 *In* Proceedings of the International Conference of Plant Protection in the Tropics. Malaysian Plant Protection Society (MAPPS), Kuala Lumpur, Malaysia.

McMahon P, Purung Hb, Lambert S, Mulia S, Nurlaila, Susilo AW, Sulistyowati E, Sukamto S, Israel M, Saftar A, Amir A, Purwantara A, Iswanto A, Guest D, Keane P. 2015. Testing local cocoa selections in three provinces in Sulawesi: (i) Productivity and resistance to cocoa pod borer and *Phytophthora* pod rot (black pod). Crop Protection 70: 28–39.

Meng X, Ouyang GC, Liu H, Hou BH, Huang SS, Guo MF. 2014. Molecular screening and predation evaluation of the key predators of *Conopomorpha sinensis* Bradley (Lepidoptera: Gracillariidae) in litchi orchards. Bulletin of Entomological Research 104: 243–250.

Posada F, Vega FE. 2005. Establishment of the fungal entomopathogen *Beauveria bassiana* (Ascomycota: Hypocreales) as an endophyte in cocoa seedling (*Theobroma cacao*). Mycologia 97: 1195–1200.

Rosmana A, Daha L, Ridayani A, Gassa A, Urling A. 2009. Persistency and penetration of entomopathogenic nematode *Steinernema carpocapsae* on surface of cocoa pod and its infectivity to cocoa pod borer *Conopomorpha cramerella* (Lepidoptera, Gracillariidae). Agritrop 28: 161–168.

Schulte MJ, Martin K, Sauerborn J. 2007. Biology and control of the fruit borer, *Conopomorpha sinensis* Bradley on litchi (*Litchi sinensis* Sonn.) in northern Thailand. Insect Science 14: 525–529.

See YA, Khoo KC. 1996. Influence of *Dolichoderus thoracicus* (Hymenoptera: Formicidae) on cocoa pod damage by *Conopomorpha cramerella* (Lepidoptera: Gracillariidae) in Malaysia. Bulletin of Entomological Research 86: 467–474.

Teh C-L, Pang JT-Y, Ho C-T. 2006. Variation of the response of clonal cocoa to attack by cocoa pod borer *Conopomorpha cramerella* (Lepidoptera: Gracillariidae) in Sabah. Crop Protection 25: 712–717.

Toxopeus H, Wiesberger G. 1983. History of cocoa and cocoa research in Indonesia. Archives of Cocoa Research 2: 7–34.

Vanialingam T, Easaw PT, Irshad M, Manals J, Cruz P. 1981. Early work in the control of the cocoa pod borer *Acrocercops cramerella* in the Philippines, pp. 345–351 *In* Proceedings of the Eighth International Cocoa Research Conference. Cocoa Producers' Alliance. Cartagena, Colombia, 18–23 Oct 1981.

Vos JGM, Ritchie BJ, Flood J. 2003. Discovery learning about cacao: an inspirational guide for training facilitators. CABI Bioscience, Surrey, United Kingdom.

Wardojo S. 1980. The cocoa pod borer – a major hindrance to cocoa development. Indonesian Agricultural Research & Development Journal 2: 1–9.

Wessel-Riemens PC. 1981. The cocoa moth pod borer (*Acrocercops cramerella* Sn.). Review and Translation of Research in Indonesia. IOCC Cocoa Research Policy Committee: 1900–1918.

Whitcomb WH. 1960. Sweet com as a trap crop to protect early tomatoes from the tomato fruitworm. Arkansas Farmer Research 9: 10. https://www.cabdirect.org/cabdirect/abstract/19600305629

Wood BJ, Fee CG, Cheong SS, Foh CC. 1992. Trials on control of the cocoa pod borer *Conopomorpha cramerella* (Snellen) in Sabah by regular complete harvesting. Tropical Pest Management 38: 271–278.

Youdeowei A. 1980. Review of cocoa pests in Indonesia and the Philippines and the development of research strategies for cocoa pest management. Developing bulk cocoa in Indonesia. Report on a visit 7 Feb–14 Mar 1980. Mimeo, Jakarta, Indonesia.

Zhang K, Fu H, Zhu S, Li Z, Weng OF, Hu MY. 2016. Influence of gamma-irradiation on flight ability and dispersal of *Conopomorpha sinensis* (Lepidoptera: Gracillariidae). Florida Entomologist 99: 79–86.