Bull. ent. Res. **65**, 263–268
Published 1975

Studies on the ecology and biology of a cocoa pollinator, *Forcipomyia squamipennis* I. & M. (Diptera, Ceratopogonidae), in Ghana

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Abstract

From field observations and laboratory rearings, the biology of *Forcipomyia squamipennis* I. & M. in cocoa plantations in Ghana was established as follows. Adult midges are found between buttresses of large shade trees, in crevices of decayed old logs, in hollow tree stumps and cocoa husk heaps. Swarming takes place at any time during the day in or around the resting place, while dispersal occurs in the early morning and in the late afternoon, the normal flight range being 5–6 m. The largest populations occur in the rainy season. Eggs are laid on moist decomposing wood, cocoa husks and other plant debris in batches of 40–90; the larvae hatch in 2–3 days and pupate after four moults, when about 12 days old; the pupal stage lasts 2–3 days. Adult females require liquid plant food for survival and oviposition, although the maturation of ova is independent of adult food intake or mating; unfertilised eggs do not develop. The maximum adult life span for both sexes is eight days in captivity. *F. squamipennis* undergoes at least 12 generations a year. Due to its abundance and continuous breeding in cocoa plantations, *F. squamipennis* is probably the most important Ceratopogonid cocoa pollinator in Ghana. Both sexes are efficient pollinators, but four times more males than females visit cocoa flowers.

Introduction

Since the discovery of Ceratopogonids as cocoa pollinators by Billes (1941), entomologists have been looking, with little success, for the breeding places of these important insects (Saunders, 1956; Soria, 1970; Winder & Silva, 1972). In 1972, one cocoa pollinator, *Forcipomyia inornatipennis* (Aust.), was discovered in Ghana breeding in goat dung in a village yard, and its biology was described (Kaufmann, 1974). Since then, breeding places of ten other known pollinators, *F. clastrieri* Dessart, *F. ashantii* I. & M., *F. squamipennis* I. & M., *F. biannulata* I. & M., *F. armaticrus* Kieff., *F. falcinella* (Kieff.), *F. seneveti* Kieff., and a few species of *Atrichopogon,* have been found (author's unpublished data). This paper presents aspects of the ecology and biology of *F. squamipennis,* an important cocoa pollinator in Ghana; this is done with a long-term view to improving pollination, by encouraging the insect's natural breeding and by mass rearing it in the laboratory for subsequent release into cocoa plantations.

Observation sites

Data on pollination of cocoa by Ceratopogonids were obtained at Tafo Cocoa Plantation, and observations on the biology of *F. squamipennis* were made in a 20-m²

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plot of Amazon–Amelonado cocoa hybrids at one-metre spacing in Bunso Cocoa Plantation (16 km from Tafo). The hybrid trees blossomed throughout the year (*cp.*, the February–May flowering of pure Amelonados), while the close spacing resulted in shade and high humidity which are necessary features of a habitat of *F. squamipennis*. The plot also contained large shade trees with deep buttresses, old stumps and decayed logs, all of which served as breeding places for the pollinator.

Materials and methods

In order to obtain the eggs of *F. squamipennis* for laboratory rearing, a plywood box (60 × 30 × 30 cm) was lined at the bottom with 5 cm of wet soil and then filled with pieces of moist, rotten (blackened) cocoa-pod husks. This provided an artificial oviposition site, and the husks were easily obtainable and conveniently searched for larvae and pupae. The box was taken to the observation site at Bunso and placed near old logs or tree stumps for a week before being taken back to the laboratory. No effort was made to locate the microscopic eggs and early-stage larvae in the box, but pupae were easily recognised. Pieces of husks with pupae were transferred to a glass jar (10 cm diam., 9 cm deep) placed inside a cage (30 cm diam., 60 cm long) made of an iron frame covered with fine mesh curtain material (in a smaller cage *F. squamipennis* does not swarm and therefore does not mate); the cage contained the food plants of adults—flowers of *Theobroma cacao, Plumbago zeylanica* and of *Vinca rosea,* and sugar solution. Emerged adults fed, swarmed, mated, and finally oviposited on the cocoa husks on which they had pupated. The newly laid eggs were subsequently removed for life-history studies.

Ceratopogonids visiting cocoa flowers were collected from June 1972 to May 1974 at one plot at Tafo twice a week between 06.30 and 09.00 h by two trained men. The insects were caught between a glass tube and its stopper, after they had alighted on the flowers.

Pollination experiments were conducted at Tafo by covering about 30 cm of a cocoa branch with a cage (15 cm diam., 30 cm long) after removing open flowers and leaving only buds on the branch (Kaufmann, 1973). For each test only 1–2 midges of the same sex were introduced into a cage. Fallen flowers inside the cage were removed daily, and these, together with those that remained on the branch after the midges had died were examined under the microscope for evidence of pollination. Flowers were regarded as being effectively pollinated when they bore 35 or more pollen grains on the style and/or stigma (D. Edwards & A. Martinson, pers. comm. 1972).

Results

Habitat

Cool, dark, moist environments such as a cocoa plantation with a closed canopy suit *F. squamipennis*, and the adults are found between buttresses of large trees, in crevices in large decayed logs, hollow rotting tree stumps and cocoa husk heaps. The trees include odahoma (*Piptadeniastrum africanum*), odum (*Chlorophora excelsa*), katawani (*Pseudospondias microcarpa*), okuri (*Bosqueia angolensis*) and silk cotton (*Ceiba pentandra*), all of which are frequently used as shade trees in cocoa plantations in Ghana. Plant debris accumulates between the buttresses of these trees; the deeper buttresses keep the debris more moist and provide the insect with an ideal year-round habitat.

Eggs

The opaque, spindle-shaped eggs of *F. squamipennis* (mean, 0·22 mm long, 0·1 mm wide at centre) are laid in loose batches of 40–90 in very moist situations, such as moss-covered rotting wood, hollow roots of dead trees, old tree holes, decayed cocoa-pod husks, etc. Dissections of wild-caught females suggest that the total number of eggs

produced per female is about 200; it seems unlikely that there is more than one gonotrophic cycle. The incubation period lasts 2–3 days at room temperatures of 20–25°C.

Larvae

The newly eclosed larvae are 0·5 mm long and semi-transparent. They feed on decayed wood, banana stems, cocoa husks and other vegetable debris in a semi-liquid state, growing to 3·5 mm long after four moults. The actual food of the larvae is said to be fungi (Winder & Silva, 1972), moulds, yeasts, bacteria (Saunders, 1956), diatoms and algae (Mayer, 1934) rather than the plant debris itself. Ecdysis in *F. squamipennis*, as in other Ceratopogonids, is difficult to observe, not only because the larvae are never quiescent before and during the process, but also because the thin transparent exuviae are hardly distinguishable against the background of plant debris. The only time the old skins can be easily found under the microscope is just after ecdysis when the spear-shaped dorsal setae (Frew, 1923; Keilin, 1918; Mayer, 1934; Saunders, 1924) of the exuviae still bear droplets on their tips.

As in *F. inornatipennis* (Kaufmann, 1974), the larvae of *F. squamipennis* are gregarious and live in a dark saturated environment; on exposure to light they disperse immediately. The last-instar larvae become waxy white as they accumulate fat bodies. The larval period is 10–15 (mean, 12) days at 20–25°C.

Pupae

F. squamipennis pupae are yellowish, 3·5 mm long, and are found in groups of 3–100 or more in the drier areas of the larval food media. With the last larval exuviae covering the last 3–4 abdominal segments, the pupae are capable of defending themselves by vigorously twisting the body when attacked (Kaufmann, 1974). The pupal period is 2–3 days at 20–25°C.

Adults

When the females emerge, the ova are only 0·08 mm long but grow to their full size of 0·22 mm after 24–36 h. Egg development is not dependent on adult food intake, for females confined in a foodless cage had fully mature eggs at their death 24–36 h after emergence. However, none of these midges laid eggs, while those provided with food, such as flowers of cocoa, *Plumbago zeylanica* and *V. rosea*, and sugar solution, oviposited under otherwise identical circumstances. The latter group survived 3–8 days as adults (3–5 days with sugar solution and/or cocoa flowers, 4–8 days with *P. zeylanica* and *V. rosea*) which suggests that the midges require plant food for survival and oviposition, although the eggs can mature without it. Newly emerged individuals of *F. inornatipennis* in a cage (1·5 × 2·0 × 1·0 m) did not prey on adults of Cecidomyiids, Drosophilids and other Ceratopogonids confined with them (Kaufmann, 1974). Similar experiments with *F. squamipennis* and a few other species produced the same results. Saunders' (1924) statement " females seem unable to mature their eggs without a meal of blood from their particular host " does not apply to this and other cocoa-pollinating species in Ghana.

Males always outnumber females. However, the male: female ratio of individuals captured from cocoa flowers was 4: 1 (sample size, 298), whereas the ratio derived from the breeding experiments was 2: 1. Similar discrepancies have been recorded for *F. inornatipennis* (Kaufmann, 1974) and *F. ashantii* (author's unpublished data).

Mating pairs are formed during swarming; they are usually seen at dusk, but also at dawn or in late afternoon. In captivity, no mating took place until two days after emergence. A male often mates with 2–3 females during one swarming, copulation lasting for a minute or two only. After mating, a female may remain within her original resting site or take off immediately to lay her eggs elsewhere. Thus, mating, as well as food, is necessary for successful oviposition; unfertilised eggs did not develop into mature larvae. There are at least 12 generations of this insect a year.

Swarming and dispersal

Swarming takes place frequently at any time of day in or just outside resting places such as old tree holes where adults congregate in groups of a dozen to 90 or more, depending upon the space available. A swarm comprises from a few to some 50 individuals of both sexes, and normally lasts for a few minutes only. Very often, swarming is caused by other insects (other Ceratopogonids, Cecidomyiids, Hymenopterans, Drosophilids, butterflies, etc.) accidentally entering the resting place occupied by *F. squamipennis* adults. When this happens, the midges become disturbed, swarm for a few minutes, and then resettle. At other times, one or two midges suddenly begin flying and are joined by others. Swarming sometimes (in 11% of 83 swarms observed) leads to mating,

The midges disperse one at a time from their resting place between dawn and 09.00 h and between 16.00 and 18.00 h. Groups present in one habitat at dusk one day are normally present on the following morning, although the individuals in each group may change. Little or no dispersal was observed after dark and during the night. The normal flight range is 5–6 m, but the midges may cover several times this distance by resting on the branches or flowers of cocoa between flights. The most favourable weather for this activity is a calm, cloudy day, for unlike *F. inornatipennis* (Kaufmann, 1974), *F. squamipennis* does not tolerate the sun and is therefore unlikely to travel freely from one cocoa plot to another. Under an overcast sky, the midges fly about actively until after 09.00 h, whereas on a bright sunny morning they become inactive earlier. No dispersal occurs in rain or strong wind.

Populations

The zigzag flight of Ceratopogonids and the conspicuous black and yellow body of *F. squamipennis* make this species fairly easy to recognise in flight. In 67 observations during April–June 1973, between 07.00 and 08.00 h, I observed 36–47 (mean, 40) individuals of *F. squamipennis* flying out of one shade tree, *Piptadeniastrum africanum*. With a dozen such trees and other resting places, the 20-m^2 plot must have contained at least several hundred midges. Although *F. squamipennis* is abundant and breeds throughout the year, its population fluctuates seasonally. Larvae are abundant during the rainy season, but during the dry season they become restricted to the relatively few niches that do not dry out.

Enemies

Natural enemies of *F. squamipennis* include mites, Collembolans, ants, Dermapterans, and centipedes. Of these, the last three are active predators of larvae and pupae, while Collembolans feed on them only when no resistance is met. The most abundant and perhaps the most destructive, however, are pale orange Trombiculid mites which breed wherever the midges breed. I once observed a batch of about 80 *F. squamipennis* eggs sucked dry by one of these mites in less than 20 min. On the same day, another batch of 70 eggs was laid; all had 'disappeared' by next morning. Not only eggs but also adults are sometimes attacked by the same species: a few adult midges caught from cocoa flowers carried as many as three mites per midge, firmly attached to their abdomen and clearly visible to the naked eye. Mayer (1934) mentions mould, Sporozoa and nematodes as entoparasites of Ceratopogonids.

Pollination

F. squamipennis is probably the most important of the Ceratopogonid cocoa pollinators because (1) it is the most abundant species (Table I), (2) it breeds within a cocoa plantation throughout the year, whereas some of the others do not, and (3) it has not been observed visiting other flowers or plants in the vicinity of the plantation. It shares this habit with *F. clastrieri, Atrichopogon* sp. (1) and *Stilobezzia africana* which are much less numerous; *F. inornatipennis, F. ashantii, Atrichopogon* sp. (2) and *Culicoides*

TABLE I. *Numbers of* F. squamipennis *and of the seven most common Ceratopogonids caught from cocoa flowers, Tafo, 1973*

Month	*F. squami-pennis*	*F. clastrieri*	*F. inornati-pennis*	*F. ashantii*	*A.* sp. (1)	*A.* sp. (2)	*S. africana*	*C. citroneus*
Jan	5	0	2	0	0	0	1	0
Feb	12	0	0	1	0	5	2	2
March	3	0	0	1	0	12	0	1
April	7	0	3	6	2	1	1	1
May	3	1	3	13	0	0	1	1
June	20	2	2	8	0	0	0	0
July	16	1	0	1	1	0	0	1
Aug	8	1	0	0	0	0	0	0
Sept	6	1	0	0	1	0	0	1
Oct	8	0	2	0	1	0	1	0
Nov	20	3	0	2	2	0	4	4
Dec	14	1	0	3	0	0	13	1
Totals	122	10	12	35	7	18	23	12
%	51·0	4·2	5·0	14·6	3·1	7·5	9·6	5·0

citroneus C., I. & M. have been seen at the flowers of *Plumbago zeylanica, Galphimia glauca, Duranta plumieri,* and leaves of *Alternanthera* sp. and *Citrus* which grow in open, sunny areas. The manner in which *F. squamipennis* pollinates cocoa flowers has already been described (Kaufmann, 1975).

Field experiments showed that males and females did not differ significantly in pollination efficiency, but the males visited fewer flowers than did the females (Table II). However, at Tafo, four times more males than females visited cocoa flowers; clearly the males of *F. squamipennis* are the principal cocoa pollinators.

TABLE II. *Pollination efficiency of* F. squamipennis

No. midges tested	Sex	No. flowers exposed	No. flowers entered	% flowers entered	No. effectively pollinated	% effectively pollinated
20	♂	255	127	50·0	27	21·3
20	♀	232	186	80·2	35	18·8

Acknowledgment

Thanks are due to Dr R. H. Foote of the USDA for the identification of some of the Ceratopogonidae.

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(*First received 5 August 1974, revised 24 January 1975*)