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ECOLOGICAL STUDIES OF MOSQUITOES IN BANANA LEAF AXILS ON CENTRAL LUZON, PHILIPPINES¹

JERRY T. LANG² AND ADELA C. RAMOS³

ABSTRACT. Aedes poicilius and Ae. flavipennis were the 2 most abundant mosquito species found breeding in the leaf axils of wild bannan, Musa errans botoan, at 3 different study sites on Clark Air Base, Philippines. Breeding of both species was continuous from June to March depending on the study site. Populations peaked at the height of the SW monsoon in August and September. Aedes poicilius and Ae. flavipennis immatures survived the dry season in wet detritus at the base of axils and in the few axils retaining some free water. It ap-

peared that Ae. flavipennis had a faster development rate and a better immature survival than did Ae. poicilius. Neither species was more prevalent at a particular axil location within the banana trees sampled, and the 2 species frequently coexisted in individual axils. The distribution of both species among banana trees conformed to the negative binomial model. Other species uncommonly associated with Ae. poicilius and Ae. flavipennis in axils included: Ae. albopictus, Armigeres magnus, Ar. subalbatus, Malaya genurostris and Toxorhynchites splendens.

INTRODUCTION

Water retained in the leaf axils of various Musa spp. common to the Philippines has been reported as a habitat for certain mosquito species (Knight and Laffoon 1946, Baisas et al. 1960). The most extensive studies of mosquitoes inhabiting axils in the Philippines have been conducted in the abaca (Musa textilis Nee) growing regions of southern Luzon and in the more southerly islands of the archipelago (Baisas et al. 1960, Cabrera 1969, Cabrera and Valeza 1972, Wenceslao et al. 1972,

Cabrera and Valeza 1978). The primary impetus behind these studies has been the use of Musa axils by Aedes poicilius Theobald, an important vector of Wuchereria bancrofti. The areas in which Ae. poicilius has been implicated as a vector of human filariasis are characterized by even rainfall patterns (Cabrera 1969). In contrast to these areas, Clark Air Base (AB) and the rest of Central Luzon have distinct wet and dry seasons which strongly influence the availability of water for leaf-axil-breeding mosquitoes. Central Luzon is also essentially free of endemic bancroftian filariasis (Cabrera 1969).

The only data on mosquito larvae found in *Musa* axils from the Clark AB area are contained in the accounts of Dowell et al. (1965) and Baisas et al. (1960). In these taxonomically-oriented surveys, larval collecting was not accom-

¹ The opinions and assertions contained herein are those of the authors and are not to be construed as views of the Department of the Air Force.

² Present address: USAFSAM/EKS, Brooks AFB, TX 78235.

³ OL-AD USAF OEHL, APO San Francisco, CA 96274.

plished through a complete annual cycle of wet and dry seasons.

The purpose of the present study was to determine species composition, seasonality, relative abundance, and general habitat selection of mosquitoes breeding in leaf axils of wild banana trees (Musa errans botoan Theodoro) on Clark AB by using a standardized larval collecting technique over a one-year period. Information derived from this study defined the importance of this breeding habitat for mosquito vector species within the large American community at Clark AB.

METHODS AND MATERIALS

DESCRIPTION OF STUDY SITES, Clark AB is a 52,200 hectare Philippine military installation located approximately 96 km north of Manila on the western edge of the Central Luzon Plain. Elevation ranges from ca 150-m above sea level on the east to ca 250 m on the west. On Central Luzon, monsoon rains begin in late April or early May and end in late October or early November. The wettest period is during the peak of the SW monsoon in August. The driest and hottest time of year is from late February until late April. The dominant natural vegetation in the Clark AB area is composed of tall grasses (kogon, Imperata cylindrica and talahib, Saccharum spontaneum), groves of wild banana (Musa errans botoan) and bamboo (Bambusa vulgaris).

Three separate sites on Clark AB were sampled monthly during the study. Site 1 was located along the northern base of Lily Hill-a 30 m high hill in the central part of Clark AB covered with a thick growth of wild banana, bamboo, lantana (Lantana camara) and other vegetation. Scattered acacia trees (Acacia sp.) provided a very limited canopy over the lower-growing vegetation. Site 2 included an area on both sides of a small stream near the Clark AB Equestrian Center. A band of vegetation similar to that found at Site 1 grew along both embankments. Taller acacia trees provided considerable shade making this site the most hydric of the three. Site 3 was in a residential area on Clark AB where wild banana trees are used in ornamental plantings. Banana trees sampled at Site 3 had little shading, and this site was the most xeric of the three.

SAMPLING METHODS. Water held in the leaf axils of 20-25 wild banana trees (Musa errans botoan) from each of the 3 sites was sampled monthly for mosquito immatures over a one-year period. In some cases, the same trees were sampled several consecutive months. The sampling device shown in Fig. 1 was used throughout the study. The eyedropper end of the device was inserted into leaf axils, and water was withdrawn by the vacuum created when the syringe plunger was withdrawn. Water collected in the 100-ml graduated cylinder at the base of the sampler. Axils were not flushed after the naturally-occurring

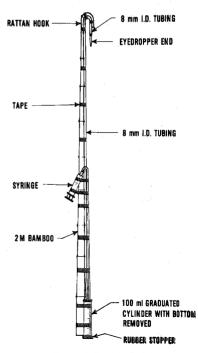


Fig. 1. Collecting device.

water was withdrawn. Trees sampled during the study ranged from 2.5 to 3.5 m in height. The number of axils sampled on an individual tree varied from 3 to 10 depending on the limitations of the sampling device and the growth habits and location of the tree. The number of dry axils and the number of axils containing water were recorded for each tree sampled. A combined total average of 450 axils were sampled each month from all 3 sites. On most occasions, water from all axils on a given tree was combined, measured for volume, and then emptied into a white enameled pan. Since the contents of each individual axil from a given tree were not examined in this phase of the study, mosquito density was measured as immatures/tree rather than immatures/ axils. All mosquito immatures were removed from the pan with an eyedropper, placed in fixative, and later identified to species.

Sampling device efficiency was crudely estimated by placing a known number of a particular immature instar of Ae. poicilius or Ae. flavipennis (Giles) into thoroughly-flushed banana leaf axils filled with tap water. After several minutes, the introduced water and immatures were withdrawn with the sampling device, and the percent recovery was recorded.

Distributions of mosquito immatures among axils at various heights were examined at Site 2 during January (dry season) and August (wet season) 1979. Axils at the extreme top, near the middle, and at the bottom of wild banana trees were sampled individually using the same sampling device. Site 2 was chosen for this aspect of the study since both Ae. poicilius and Ae. flavipennis occurred in greatest abundance there.

Developmental rates of a sample of wild-caught, first instar larvae of Ae. poicilius and Ae. flavipennis were measured individually in 10 ml glass vials containing tap water. The vials were maintained at ambient outdoor temperature (mean low 23.5°C, mean high 30°C). Larvae were fed a standard diet of finely-ground laboratory chow, lactalbumin, and brewer's

yeast (1:1:1). Development and mortality were checked each day.

To determine survival of mosquito immatures during the dry season, 4 banana trees (each containing 6-12 axils) at Site 2 were felled each month during February, March and April 1980. Any free water in the axils was removed and checked for immatures before cutting the trees down. All felled trees were taken back to the laboratory where each individual axil was carefully opened. Detritus was scraped and washed from each individual axil into separately-marked 1 liter battery jars. The freshly-removed detritus was immediately examined for mosquito immatures, and all jars were held for at least 1 week in the laboratory to detect subsequent egg hatch as evidenced by the appearance of additional larvae.

RESULTS

Sampling device (Fig. 1) efficiency was 79, 58, 56 and 31 percent for removing pupal, fourth, third and second instars, respectively, in the standardized efficiency tests. Efficiency was not measured using first instar larvae, but based on data from the other measurements, it was estimated at about 20%. Except for examining age distributions in Table 1, sampling efficiency estimates were not used in correcting for numbers of immatures collected since the effects of varying water levels, leaf axil structure, and amount of detritus on collection efficiency were not estimated. For example, it was found in the dry season study at Site 2 that mosquito immatures of various ages could survive in nonextractable thin layers of water trapped in wet detritus at the axil bases.

Rainfall at Clark AB for the period 1978-79 totalled 217.8 cm; slightly wetter than the 18-yr annual average of 177.5 cm (Fig. 2). Average daily temperature ranged from 23°C in February to 29°C in April.

Breeding habitat availability and immature mosquito abundance reflected

Table 1. Age distribution of immature mosquitoes collected from banana leaf axils on Clark AB, RP, October 1978-September 1979.

				A	Ae. flavipennis							Ae. poicilius		
		Site			Percent	Adinsted	Adineted		Site			Doncon	Adimend	A 45
nstar	-	2	3	Total	total	total*	% total	-	2	3	Total	total	rajusted total*	Adjusted % total
	81	77	0	158	16.3	395	39.6	œ	201	124	333	24.7	7. 7.	474
	139	204	-	344	35.4	277	27.8	34	484	127	645	48.0	416	. 10.
	29	88	01	149	15.3	133	13.3	16	119	7	142	10.6	200	2.5
	57	126	_	184	18.9	106	10.6	6	106	75	130	9.7	35	. 4 . x
	52	85	0	137	14.1	87	8.7	15	99	12	6	6.9	9.5	
Total	388	580	4	972		866		79	946	288	1343	;	1171	2

details)

annual rainfall patterns (Fig. 2 and 3). Only at Site 2 were significant amounts of water retained in leaf axils throughout the hot dry months of March and April 1979. Usually, it was the second or third axil from the top of the tree that contained water during the driest part of the vear at Site 2. The leaf axils at all 3 sites were refilled with rainwater in May 1979. However, axil refill was not accompanied by a sudden increase in early instar mosquito larvae, and Ae. poicilius and Ae. flavipennis populations did not return to pre-dry season levels until July or August (Fig. 3).

During the dry season, detritus and water from trees felled at Site 2 were examined. A total of 11 larvae and 17 pupae of Ae. flavipennis and 8 larvae of Ae. poicilius were found mainly in axils containing small amounts of free water or wet detritus. An additional 28 Ae. flavipennis and 3 Ae. poicilius larvae hatched from eggs contained in the wet detritus which was held in the laboratory. Very few larvae were detected when totally dry detritus was flooded in the laboratory and held for 7-10 days.

The total numbers of each Ae. poicilius and Ae. flavipennis instar collected throughout the study are given in Table 1. Although considerably more immatures of Ae. poicilius (1343) than Ae. flavipennis (972) were found, it was only the first and second larval instars that accounted for the difference. Ae. poicilius was much more successful exploiting Site 3 breeding habitats than was Ae. flavipennis, however, mortality rates for older Ae. poicilius instars at Site 3 were apparently higher than at the other sites (Table 1). When either actual collection data or collection data adjusted for estimated sampling efficiency and individual instar duration were examined with a Chi-square test, overall age distributions indicated a higher survival rate for Ae. flavipennis than for Ae. poicilius (observed data χ^2 = 115.36, df = 4, p = < .001, adjusted data $\chi^2 = 72.86$, df = 4, p = < .001) (Table 1).

The percent composition of mosquito immatures at Site 2 was 60% and 36% for

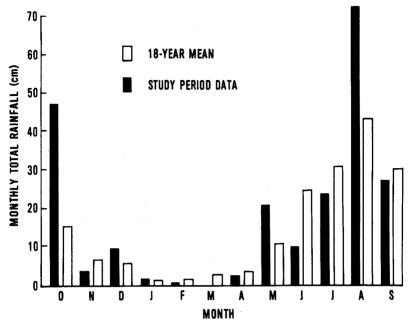
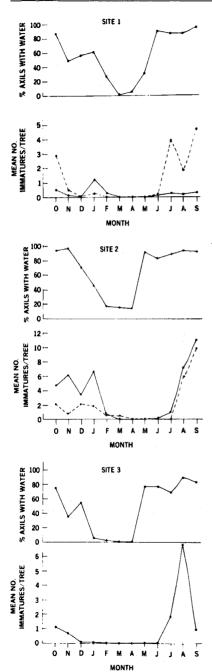


Fig. 2. Monthly total rainfall data for the study period (1978–79) compared to 18-yr means as reported by the Clark AB weather station.

Ae. poicilius and Ae. flavipennis respectively (the other 4% of the immatures belonged to different species). Aedes poicilius also predominated at Site 3 (98.6% to 1.4%). At Site 1, Ae. flavipennis immatures outnumbered those of Ae. poicilius 83% to 17%. Maximum density and resource exploitation of Ae. poicilius at Site 2 occurred in September 1979 when immatures were found in 88% of the trees sampled and the mean number of immatures/tree was 11.24 (Fig. 3). Comparable maxima for Ae. flavipennis at Site 2 during September were 92% and 9.92 immatures/tree.

The among axil distributions of Ae. poicilius and Ae. flavipennis were examined separately at Site 2 during January and August when contents of individual axils from top, middle, and bottom areas of trees were examined. Mean numbers of immatures/axil for Ae. poicilius were 3.65,

1.90 and 2.05 for top, middle and bottom axils, respectively, in January, and 0.04, 0.60 and 0.16 for corresponding axils in August, Means for Ae. flavipennis were 1.85 (top), 0.40 (middle) and 0.30 (bottom) in January and 0.72, 0.76 and 0.48 for similar axil positions in August. Data were analyzed using Friedman's nonparametric test for matched observations (Bradley 1968). There was no evidence that either species preferred a particular axil location within the trees during either time period. The within axil distributions of Ae. poicilius and Ae. flavipennis at Site 2 during January and August were examined using the method of Cole (1949). Significant positive association was found for both months ($\chi^2 = 5.34$, p = < .025 and $\chi^2 = 6.71$, p = < 0.025 for January and August, respectively) indicating that the presence of both species within individual axils occurred more frequently



than would be expected by random distribution.

When all monthly collection data from the 3 sites was pooled, the among tree distribution conformed to the negative binomial distribution (p = <.001) (Table 2). The negative binomial distribution model characterizes many insect populations living in specialized habitats subject to marked seasonal weather variations (Southwood 1978).

The developmental rates of wild-caught and individually-reared Ae. poicilius and Ae. flavipennis are compared in Table 3. Although there was a tendency for Ae. poicilus to be somewhat slower in its development than Ae. flavipennis in every instar except the pupal, significance was only shown in the duration of the first instar (p = < .05) and overall immature life (p = < .01) (Table 3). Significance was determined using Wilcoxon's Rank Sum Test.

On several occasions, other mosquito species besides Ae. poicilus and Ae. flavipennis were found breeding in the leaf axils of wild banana. These species included: 7 Ae. albopictus (Skuse), 26 Armigeres magnus (Theobald), 2 Armigeres subalbatus (Coq.), 51 Malaya genurostris Leicester, and 4 Toxorhynchites splendens (Wied). Malaya genurostris was found at all 3 sites and was most common at Site 2 during the cooler part of the dry season. Aedes albopictus, a common daytime biter at Sites 1 and 2 during the wet season, was found in banana leaf axils two times at Site 2. Armigeres magnus and Armigeres subalbatus normally preferring bamboo stumps as breeding sites (Basio 1971), utilized Site 2 banana leaf axils in the hottest and driest time of year.

The predatory larvae of Tx. splendens were found at Site 2 during the middle of the wet season in 1979 and in the middle of the dry season in 1980. Toxorhynchites

Fig. 3. Percent wet leaf axils and mean number of immatures per tree of Ae. poicilius at Sites 1, 2 and 3 (solid line) and Ae. flavipennis at Sites 1 and 2 (dashed line).

Table 2. Dispersion of Ae. flavipennis and Ae. poicilius immatures among wild banana trees.*

	Species					
	Ae. fla	vipennis	Ae. poicilius			
No. immatures	No.	trees	No. trees			
per tree	Observed	Expected**	Observed	Expected**		
0	701	700.9	684	683.9		
1	62	61.7	60	58.8		
2	28	31.0	31	30.2		
3	21	19.9	14	19.9		
4	16	13.1	17	14.5		
5	14	10.6	8	11.2		
6	9	8.2	9	8.9		
7	3	6.6	9	7.3		
8	5	5.4	3	6.1		
9	3	4.4	10	5.2		
10	7	3.7	4	4.5		
>10	21	23.9	39	37.2		
Total	890	890	888	888		
Chi. Sq., df, p		7.43, 9, NS		9.66, 9, NS		
$\mathbf{m} = \mathbf{x}$		1.06		1.51		
S^2		13.2314		25.6076		
k		.0959		.0911		

* Data pooled for entire study period from all 3 sites.

** Negative binomial distribution having parameters m and k, estimated by $\hat{m} = \tilde{x}$ and k (Bliss 1953).

splendens and Ae. albopictus but not Ae. poicilius or Ae. flavipennis oviposited in CDC ovitraps (Fay and Eliason 1966) set at ground level in banana groves at Site 2 during the end of the wet season (October and November 1979).

Table 3. Median developmental times for individually-reared Ae. flavipennis and Ae. poicilius.

	Species					
Instar	fla	Ae. vipennis	Ae. poicilius			
	n	Median (days)	n	Median (days)		
1* 2 3	17	2	22	3		
2	7	4	11	- 5		
3	6	2	10	. 3		
4	5	3	9	4		
Pupae	4	2	. 9	2		
Total						
Developmental						
Time	4	13	9	17		

* Estimated since wild-caught 1st instar larvae were used.

In addition to mosquito larvae, at least 2 species of Clogmia (Psychodidae: Psychodinae) were commonly found in the wild banana leaf axils. Immatures were counted in the same manner as the mosquitoes and exhibited similar seasonal population fluctuations.

DISCUSSION

Rainfall, through its effect on leaf axil moisture levels, was the most important factor regulating population densities of mosquito immatures in banana leaf axils on Clark AB. During the dry season, upper axils appeared most likely to retain water. This phenomenon was probably related to axil size and associated surface area, water tightness of the axil, shading and dew condensation. During studies of Ae. simpsoni (Theobald) immatures in Africa, Teesdale (1957) also reported that upper leaf axils in banana trees were most likely to retain water in the dry season.

The lag between axil refill in May and

marked increases in population densities of Ae. poicilus and Ae. flavipennis in July and August probably reflects a dry season survival strategy in which relatively few larvae and pupae persist among the few leaf axils capable of retaining some moisture. It does not appear that large numbers of eggs survive in dry axils and hatch when flooded by the first monsoon rains since immature populations would be expected to increase more rapidly than observed (Fig. 3).

Site differences in the relative abundance of Ae. poicilius and Ae. flavipennis were probably the result of several interacting factors. Site 2 appeared to be the most favorable area for both species and also had the most diverse flora and fauna. This diversity along with the more hydric nature of Site 2, presumably provided adult mosquitoes with a greater variety of hosts and suitable resting places and moderated the dry season's adverse impact on immature mosquito populations. Site 3 was the harshest of the 3 sites from the standpoint of dry season severity. Banana trees unprotected from sun and wind lost moisture from axils very quickly at the end of the rainy season (Fig. 3). Likewise, protected resting sites for adults were scarce and host diversity was reduced. The ready availability of human hosts at Site 3 may partially explain the predominance of the more anthropophilic Ae. poicilius (Cabrera and Arambulo 1973, Cabrera and Valeza 1978). Additionally, Ae. poicilius and Ae. flavipennis may differ in their susceptibility to malathion fogging conducted at this

The positive association of Ae. poicilius and Ae. flavipennis immatures of all ages within individual axils at Site 2 indicates that competition between the 2 species is not intense. No attempt was made to determine how immatures coexisting within individual axils partition resources. The apparent overall higher survival rate of Ae. flavipennis compared to Ae. poicilius may partially result from a significantly shorter development time (Table 3) which, if occurring under field condi-

tions, would reduce the length of exposure of Ae. flavipennis to instar-specific mortality factors. The second larval instar of both Ae. poicilius and Ae. flavipennis was apparently the most time-extended stage of development and correspondingly fewer survived this instar (Table 3).

Except for Ml. genurostris, utilization of banana leaf axils by the rest of the species collected was considered spurious and probably related either to increased female searching behavior triggered by water shortage in more preferred oviposition habitats or to chance location of the banana leaf axils made more likely by relatively high populations of gravid females during favorable periods.

Similarities are very strong between the bionomics of Ae. poicilius and Ae. flavipennis immatures on Central Luzon and the bionomics of Ae. simbsoni immatures in tropical Africa (Teesdale 1957, Pajot 1978, Brown and Bang 1980). Like Ae. poicilus and Ae. flavipennis, Ae. simpsoni uses banana leaf axils as a preferred breeding site (Teesdale 1957, Gillett 1972, Pajot 1978). In African areas with wet and dry seasons, the availability of Ae. simpsoni breeding habitat, i.e. water containing leaf axils, and fluctuations in populations of Ae. simbsoni immatures follow patterns similar to that of Ae. poicilius and Ae. flavipennis on Central Luzon (Teesdale 1957). Likewise, dry season survival of Ae. simpsoni larvae in minimal amounts of water within leaf axils was reported by Teesdale (1957) and Pajot (1978). Mean numbers of larvae/ plant for Ae. simpsoni over a one year period ranged between 0 in dry periods to 10-12 during and immediately after rainy periods (Brown and Bang 1980). This was the same range in which Ae. poiciluis and Ae. flavipennis immature populations fluctuated during our study (Fig. 3). Brown and Bang (1980) found immatures of Malaya spp. most commonly associated with Ae. simpsonisimilar to our findings of association between Ml. genurostris and Ae. poicilius and Ae. flavipennis. In Africa, Eretmopodites spp., a predaceous mosquito occasionally found in leaf axils with Ae. simpsoni, appears to occupy a similar niche to Tx. splendens on Central Luzon. Like Tx. splendens, Eretmopodites spp. does not appear to have a major impact on densities of prey species inhabiting leaf axils (Pajot 1978).

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