

Relative population densities of *Aedes albopictus* and *A. guamensis* on Guam

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Aedes guamensis Farner & Bohart is indigenous to Guam but *A. albopictus* is known to have arrived in 1944. The larval ecology of the two species is very similar; both species breed in tree holes, coconut shells, and other natural and man-made water containers. The purpose of the study was to compare the relative densities of larval populations of the two species with those determined in a survey made in 1948-49. The results suggest that as the population density of *A. albopictus* increased, that of *A. guamensis* decreased by as much as about 95% in artificial containers, and by 30% or more in natural breeding habitats. Since there seems to be no environmental factor involved in rendering the breeding places unsuitable for *A. guamensis*, the reduction in *A. guamensis* populations may be, in part, the result of competition from *A. albopictus*.

Aedes guamensis Farner & Bohart (subgenus *Stegomyia*) is indigenous to Guam and other islands of the Mariana group. Since its most characteristic breeding habitat appears to be rot holes in trees, it is abundant in heavily wooded areas, which may be remote from human habitation. The larvae are also found in water trapped in coconut shells and in certain other plant cavities. Bohart & Ingram (1946) stated that *A. guamensis* is not a domestic mosquito, and that in a survey made in Guam in 1945 the larvae were never found closer than about 15 m to houses although "suitable containers" were present. In a survey made in 1948-49, Reeves & Rudnick (1951) frequently found the larvae in tin cans, rain barrels, and other artificial containers, and also observed that one-third of these containers were within about 30 m, and one-fifth within about 15 m, of houses. Some of the containers were actually leaning against the side of a house.

In 1944 there was an extensive outbreak of dengue on Guam. An intensive survey by Bailey & Bohart (1945) revealed that *A. aegypti* was abundant in all kinds of artificial container close to houses, but it was never found in association with *A. guamensis*. A control campaign resulted in the apparent eradication of *A. aegypti* from the island (Bohart & Ingram,

1946). Reeves & Rudnick (1951) suggested that the decrease in control measures around houses after the *A. aegypti* control campaign might have produced conditions that would enable *A. guamensis* to move into the peridomestic environment and utilize tin cans and other receptacles associated with human activities as breeding habitats. It is possible that the elimination of *A. aegypti* created a biological vacuum that *A. guamensis* was starting to fill.

According to Hull (1952), *A. albopictus* (Skuse) was first discovered on Guam (at Ylig Bay and Yona) in 1944 by A. B. Weathersby. The species apparently remained rare for some time thereafter, and it was not recorded by Baily & Bohart in 1945. The species was found by Yamaguti and LaCasse at Yona in March 1948 (Bohart, 1956). In 1948 and 1949, Reeves & Rudnick found *A. albopictus* in many localities in the northern two-thirds of the island, and Bohart (1956) found it in the southern part (Merizo) in 1951. Bohart refers also to collections made in 1952 by Gressitt in Tutujan and by Hu on Mt Santa Rosa.

It is evident that *A. albopictus* has become widespread in Guam. Larvae of this species are abundant in the water that collects in troughs formed by split bamboo stems, in stumps of cut bamboo, and in coconut shells that have been opened by rats or man. The larvae occur not infrequently in tree holes although this habitat appears to be less attractive than the others. The species readily makes use of

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various artificial containers in the immediate vicinity of houses, as well as those in woods and other areas farther from human habitation.

In laboratory experiments, *A. albopictus* kept in both small and large cages was observed to reduce greatly, or even to eliminate, competing populations of *A. polynesiensis* Marks (Gubler, 1970; Rozeboom, 1971). The situation on Guam offers an opportunity to observe whether *A. albopictus* has a similar effect on *A. guamensis*. Both *A. guamensis* and *A. polynesiensis* are members of the *A. scutellaris* subgroup, and their breeding habitats are very similar to those of *A. albopictus*. In theory, ecological homologues cannot coexist (de Bach, 1966). The purpose of the recent survey was, therefore, to attempt to measure the relative densities of the two species in their various habitats, and to determine whether the population density of *A. guamensis* had undergone a reduction, especially in the peridomestic environment previously inhabited by *A. aegypti*.

MATERIALS AND METHODS

The survey was conducted on 17–31 July 1970 and on 16–20 November 1970. The first period was in the early part, and the latter was towards the end, of the rainy season. These are the most favourable times of the year for the development of these species, which depend upon rainfall to fill the small container habitats with water. Since *A. guamensis* females are not readily attracted to human or other bait, adult biting catches could not be used to measure the relative abundance of the two species. Nevertheless, adults were captured as they came to bite while the larval collections were being made. Light trapping is also not a satisfactory method of collecting these two species; therefore, it was necessary to rely on larval collections. All kinds of natural and artificial breeding habitats were examined. Selected areas included woods, coconut groves, bamboo thickets, and fields and premises adjacent to, or several hundred metres from, houses. An effort was made to obtain a complete census of each breeding container, but in a few collections from large containers it was possible to obtain only a sample.

All larvae and pupae were taken to the laboratory for identification. During the early part of the survey, when more time was available, many of the larvae were reared to the adult stage; adults were obtained also from the pupae and the identification of these specimens was based on the distinctive adult markings. In the November collections, limited time and

resources permitted the rearing of adults from pupae only; thus most specimens were identified as larvae. Larvae of *A. albopictus* have long anal gills, all 4 being approximately equal in length. The anal gills of *A. guamensis* larvae are short; the lower pair are shorter than the upper pair and are often almost bud-like. The separation of the larvae was based on the character of the anal gills, which appeared to be distinctive in not only the third and fourth instars but also in the second instar and even the first stages. Another characteristic feature is the lateral hair on the anal saddle; in *A. albopictus* it is double while in *A. guamensis* it has 3 or more branches. However, this was useful as a confirmatory character for the third- and fourth-stage larvae only.

Larvae were killed in hot water and identified immediately under a dissecting microscope. A blue glass filter placed underneath the shallow dish containing the larvae greatly enhanced the visibility of the gills.

In order to evaluate a change in population densities, it was necessary to compare the results of the latest survey with those of Reeves & Rudnick (1951). Through the generous cooperation of Dr Reeves, it was possible to examine the original collection records. In the 1948–49 survey, complete larval counts were not made, samples being taken instead. The actual numbers of specimens were recorded for some collections but for the others use was made of a frequency-distribution table, which was part of the collection sheets. The collector marked the box corresponding to his estimate of the number of larvae and pupae in the container, i.e., 0–1, 1–5, 10–20, etc. In our calculations of the relative numbers of larvae in each collection, the largest number was assigned to *A. albopictus* and the smallest to *A. guamensis*. Thus, if both species had been collected, and the 10–20 box marked, it was assumed that 19 specimens were *A. albopictus* and only 1 was *A. guamensis*. If only *A. albopictus* had been collected, and the 1–5 box marked, 5 larvae of this species were counted; however, if only *A. guamensis* was found, only 1 larva was counted. The reason for this procedure was to make certain that an increase in *A. albopictus* and a decrease in *A. guamensis* densities in the 1970 survey would not be influenced by an underestimate of *A. albopictus* and an overestimate of *A. guamensis* in the 1948–49 survey.

For purposes of comparison, the numbers of larvae calculated for 1948–49 are given in Table 1. The table also shows the actual numbers of collections recorded by Reeves & Rudnick (1951).

Table 1. Collections of *A. guamensis* and *A. albopictus* in the 1948–49 survey *

Containers	No. of collections		<i>A. albopictus</i>		<i>A. guamensis</i>	
	<i>A. albopictus</i>	<i>A. guamensis</i>	No.	%	No.	%
natural						
tree holes	2	36	16	6.7	222	93.3
coconut shells	20	20	195	56.7	149	43.3
hollow log	1	1	9	90.0	1	10.0
rock holes	1	2	1	16.7	5	83.3
totals	24	59	221	37.0	377	63.0
artificial						
cans	8	23	22	17.7	102	82.3
large ^b	31	41	120	49.0	125	51.0
household ^c	18	30	83	64.8	45	35.2
tires	21	36	101	46.1	118	53.9
miscellaneous ^d	8	10	72	55.4	58	44.6
totals	86	140	398	47.0	448	53.0
combined totals	110	199	619	42.9	825	57.1

^a Numbers of collections taken directly from Table 7 of Reeves & Rudnick (1951); number of specimens based on calculations from original records (see text); hollow log and rock hole counts from original records.

^b Barrels.

^c Bowls, pots, biscuit tins.

^d Discarded vehicle bodies, scrap metal dumps, helmets, oil drums.

RESULTS

Additional locality records

A. albopictus has been collected in several localities that do not appear to have been listed in earlier surveys. They include Tarague Beach, Cetti Bay, Route 4 at La Sa Fua River, Talona, Inarajan, and about 1 km inland from Talofofu Bay. Evidently, *A. albopictus* has invaded most of Guam.

Adult human collections

As reported by previous workers, *A. guamensis* is rarely observed biting human bait. *A. pandani* was the most abundant mosquito but *A. albopictus* adults could have been collected in large numbers if an effort had been made to do so.

Collections from breeding habitats

Table 2 shows the number of times the two species were collected, i.e., the number of positive collec-

tions as well as the number of specimens. In these records, a single first-stage larva of *A. guamensis* was scored as an occurrence. A more revealing measurement of the relative densities of mosquitos is the actual numbers of larvae and pupae taken from the breeding habitats.

The preference of *A. guamensis* for tree holes is very evident; of the 24 holes in which larvae were found, *A. guamensis* was present in 20 and *A. albopictus* in only 13. Of a total of 598 *A. guamensis* larvae found in natural habitats, 332 (56%) were in tree holes. Furthermore, in 5 of these holes there was a total of 195 *A. guamensis* but no *A. albopictus*. The high organic content of the water appeared to be attractive to the former species but repellent to the latter. Nevertheless, *A. albopictus* is not uncommon in tree holes, including small, narrow cavities containing only a few ml of water.

Altogether, 68% of specimens from all natural breeding habitats and 82%, 75%, and 88%, respec-

Table 2. Collections of *A. albopictus* and *A. guamensis* from breeding habitats in 1970

Containers	No. of positive containers	No. of collections		<i>A. albopictus</i>		<i>A. guamensis</i>	
		<i>A. albopictus</i>	<i>A. guamensis</i>	No.	%	No.	%
natural							
tree holes	24	13	20	126	27.5	332	72.5
bamboo	21	21	8	381	82.1	83	17.9
coconut shells	38	36	18	432	75.0	144	25.0
palm bracts	9	7	4	267	87.8	37	12.2
hollow log	1	1	1	3	60.0	2	40.0
snail shells	9	9	0	50	100	0	0
rock holes	1	1	0	8	100	0	0
totals	103	88	51	1 267	67.9	598	32.1
artificial							
cans	76	74	6	1 080	93.1	80	6.9
large ^a	8	8	2	373	97.4	10	2.6
household ^b	10	10	1	286	99.7	1	0.3
tires	7	7	6	2 594	95.4	125	4.6
miscellaneous ^c	20	19	3	362	98.9	4	1.1
totals	121	118	18	4 695	95.5	220	4.5
combined totals	224	206	69	5 962	87.9	818	12.1

^a Barrels, tubs, buckets.^b Bowls, pots, biscuit tins.^c Glass jars, bottles, rubber boot, metal trough, etc.

tively, of the larvae and pupae from bamboo, coconut shells, and palm bracts belonged to the species *A. albopictus*. It is of interest to note that shells of the giant African snail, *Achatina fulica* Bowdich, lying on the ground in wooded areas, often contain *A. albopictus* larvae and pupae.

The predominance of *A. albopictus* is far more striking in collections from artificial containers, the species being over 6 times more frequent than any other; in tin cans the ratio was more than 12:1. Of 4 695 specimens in artificial containers only 4.5% were *A. guamensis*, and there were only 80 *A. guamensis* in the 76 tin cans that were positive for larvae. Furthermore, 62 of these specimens came from a large tin can (about 2 litres capacity) partially buried in mud, heavily shaded by a dense canopy of low tree branches, and containing a thick deposit of decaying leaves and other debris. Ecologically, this

habitat was probably more nearly related to a tree hole. Except for 7 larvae of *A. oakleyi*, the can contained only *A. guamensis*. If this collection is excluded, only 18 *A. guamensis*, larvae and pupae, i.e., less than 2% of the total number, were taken from cans.

Of the artificial containers, tires were the most prolific source of *A. guamensis*. The respective numbers of *A. albopictus* and *A. guamensis* from 5 of the 7 tires examined were as follows: 395, 38; 259, 14; 207, 7; 929, 35; 782, 30. Three of the tires were lying within 15–30 m of a house, and two were at the edge of a clearing that appeared to be at least 1 km distant from any dwelling.

A comparison of larval associations found in the 1970 survey with those reported by Reeves & Rudnick (1951) is presented in Table 3. In the earlier survey, *A. albopictus* was collected more frequently with

Table 3. Larval associations in breeding habitats; comparison with results of Reeves & Rudnick (1951)

Survey	Habitat	No. of combinations ^a		Percentage ^b	
		<i>A. albopictus</i>	<i>A. guamensis</i>	<i>A. albopictus</i>	<i>A. guamensis</i>
1970	natural	34/88	34/51	38.6	66.7
	artificial	13/118	13/18	11.0	72.2
	totals	47/206	47/69	22.8	68.1
1948-49	totals	25/54	25/92	46.3	27.2

^a Numerator = number of times a species was taken in combination, denominator = total number of collections for this species.

^b Percentage occurrences of indicated species in combination with the other species.

Table 4. Proximity of collections to houses

	Collections and specimens at indicated distance				Totals
	3-30 m	30-90 m	90-450 m	0.8 km or more	
NATURAL CONTAINERS					
no. of collections ^a	9	4	47	43	103
no. including <i>A. albopictus</i>	9	4	44	31	88
no. including <i>A. guamensis</i>	2	2	17	30	51
specimens					
totals	101	113	903	748	1 865
<i>A. albopictus</i> (%)	95.0	92.9	76.8	49.7	68.0
<i>A. guamensis</i> (%)	5.0	7.1	23.2	50.3	32.0
ARTIFICIAL CONTAINERS					
no. of collections ^a	78	3	21	19	121
no. including <i>A. albopictus</i>	77	3	20	18	118
no. including <i>A. guamensis</i>	12	0	2	4	18
specimens					
totals	2 487	11	291	2 126	4 915
<i>A. albopictus</i> (%)	94.4	100.0	97.9	96.5	95.5
<i>A. guamensis</i> (%)	5.6	0	2.1	3.5	4.5

^a Numbers of collections and numbers of times *A. albopictus* and *A. guamensis* were found in these collections.

A. guamensis—46.3% in 1948–49 as against 22.8% in 1970. On the other hand, in 1948–49 *A. guamensis* was less often found in association with *A. albopictus* (27.2% against 68.1%).

Proximity to houses

In Table 4 the collection data have been rearranged to show the proximity of mosquito breeding places to human habitations. It can be seen that in natural containers the frequency and density of *A. guamensis* increases with the distance from houses. In artificial containers there was no correlation between the abundance of either species and proximity to houses.

DISCUSSION

In their 1948–49 survey, Reeves & Rudnick (1951) identified larvae of *A. guamensis* and *A. albopictus* in 203 and 113 collections, respectively. The increase in the distribution and abundance of *A. albopictus* in Guam is quite evident from the results of our survey. Formerly, *A. guamensis* was more often the species inhabiting breeding places that it now shares with *A. albopictus*. On the other hand, *A. albopictus* now occurs more often in single populations.

Most of the single populations of *A. guamensis* occurred in tree holes, and in some of these the water was foul or contained a heavy accumulation of organic debris; this may have been a factor in excluding *A. albopictus*. Furthermore, this kind of habitat may be a residual "ecological niche" in which *A. guamensis* can survive without competition from *A. albopictus*. However, even in such habitats the ratio of *A. albopictus* to *A. guamensis* larvae and pupae was over 10 times that observed in 1948–49, i.e., 1:1.5 against 1:18. Reeves & Rudnick (1951) made many of their tree-hole collections near human habitations and they considered that if they had searched more extensively in jungle areas, the proportion of *A. guamensis* would have been much higher. Their original collection records show that at least 18 of the tree holes in which *A. guamensis* were found were situated at a distance of 1.5–30 m from houses. The two tree holes containing *A. albopictus* were 15 m from a house. In the 1970 survey, only 2 tree holes within 15 m of a house were sampled, and they contained only *A. albopictus*. It is possible that if more collections had been made near houses, the proportion of *A. albopictus* would have been much higher.

The ratio of *A. albopictus* to *A. guamensis* in coconut shells was 1:1 in 1948–49, and 2:1 in the

1970 survey. The calculated proportions of larvae were 56.7% and 43.3% in 1948-49 while in 1970 75% were *A. albopictus*. A comparison of all collections from natural breeding habitats shows that whereas in 1948-49 *A. albopictus* represented 37% of the total population, the proportion had increased to 68% in 1970.

The difference between the relative numbers of occurrences and larval densities in artificial containers in the two surveys is far more striking. The ratio of *A. albopictus* to *A. guamensis* increased from 1:1.6 to 6.6:1; in cans the ratio was 1:2.9 against 12.3:1.

In 1970 a total of 4 915 specimens were collected from artificial containers; 95.5% were *A. albopictus* and 4.5% were *A. guamensis*. In 1948-49 the calculated proportions of these species were 47% and 53%, respectively. The calculated numbers of *A. albopictus* and *A. guamensis* larvae in cans in 1948-49 were 22 and 102 while in 1970 the actual numbers were 1 080 and 80 (including the 62 from the atypical can). Thus in 1948-49 over 80% of the larvae in cans were *A. guamensis* but in 1970 only about 7% belonged to this species.

The question, however, is not whether there has been an increase in the population density of *A. albopictus*, but whether there has been a decrease in the density of *A. guamensis*. Unfortunately, a census is not available for the populations that occurred in former years; in the survey made by Reeves & Rudnick (1951), samples of larvae and pupae only were taken. Nevertheless, these stages were randomly selected, and should reflect the relative densities of the two species. From the original records, it was calculated that in artificial containers, 47% of the specimens were *A. albopictus* and 53% were *A. guamensis*. These calculations gave the maximum possible densities for *A. albopictus* in the 1948-49 survey, and it seems justified, for the sake of simplicity, to consider this as a 50:50 ratio. Thus, there were 100 *A. guamensis* larvae for every 100 *A. albopictus* larvae captured, but in the recent survey there were only 4 or 5 *A. guamensis* larvae for every 100 *A. albopictus* larvae. This implies that for every 100 *A. guamensis* larvae found formerly in artificial containers, there now are only 4 or 5. If indeed the density of *A. guamensis* is now only 5% of its former level, this species has undergone a reduction of about 95% in artificial container habitats.

It is necessary to ask whether this reduction has been the result of further changes in the environment or of competition with *A. albopictus*. The fact that

some *A. guamensis* larvae and pupae were taken from artificial containers near houses shows that these breeding habitats have not become unsuitable; no environmental factors could be detected that would have caused a reduction of the *A. guamensis* population in artificial containers near, or even some distance away from, human habitations. Many of the containers were in environments where, irrespective of the proximity of houses, conditions should have been favourable for *A. guamensis*.

In forests and coconut groves situated far from permanent dwellings, *A. guamensis* is maintaining itself, especially in tree holes. The species seems to be capable of existing in water with a higher content of decomposing organic material than that preferred by *A. albopictus*. Even so, there appears to be a steady encroachment by *A. albopictus* into these habitats. It was calculated that in 1948-49, 63 of every 100 larvae from natural breeding places belonged to the species *A. guamensis* but in the recent survey only 32 of every 100 larvae from natural containers were of this species. This indicates a reduction of about 50%.

The possibility should also be considered that instead of a decrease in the density of *A. guamensis*, there was only an increase in that of *A. albopictus*. However, to judge from the size of the larval populations in those localities where *A. albopictus* had become established, it appears unlikely that even in 1948-49 the *A. albopictus* larval populations, existing at a 1:1 ratio with those of *A. guamensis*, would have been as small as the present populations of *A. guamensis*, especially in artificial containers. In a survey made in 1951, Hull (1952) collected *A. albopictus* 117 times and *A. guamensis* 17 times. Although Hull (*op. cit.*) did not determine the relative larval densities, the ratio of *A. albopictus* to *A. guamensis* in his collections is actually higher than the ratio we obtained. This implies not only that larval densities of *A. albopictus* were high and possibly comparable to those we observed, but also that there was a considerable replacement of *A. guamensis* by *A. albopictus* between 1949 and 1951. It is of interest also to refer to Hull's conclusion that *A. albopictus* was more successful than *A. aegypti* as a competitor of *Culex quinquefasciatus*.

It is recognized that in the absence of more thorough larval censuses in previous years, certain assumptions must be made; the conclusions reached can therefore be only tentative. Nevertheless, there seems to have been a change in the relative proportions of the two species, brought about by an appar-

ent increase in the density of *A. albopictus* and a reduction in that of *A. guamensis*, especially in artificial containers. This may have been caused by a change in the environment that we were unable to detect. Another possibility is that on Guam a natural

experiment may be taking place in relation to competitive exclusion between two mosquito species that are almost, if not exactly, ecological homologues. A reexamination of the developments in the future may be of considerable interest.

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RÉSUMÉ

DENSITÉS RELATIVES DES POPULATIONS D'*Aedes albopictus* ET D'*Ae. guamensis* À GUAM

Aedes guamensis, espèce indigène de Guam et d'autres îles de l'archipel des Mariannes, est essentiellement un moustique des régions boisées. Cependant, en 1948/49, on a constaté sa présence dans des gîtes naturels ou artificiels à proximité immédiate des habitations, où il a probablement pris la place d'*Ae. aegypti*, éliminé en 1946. *Ae. albopictus*, décelé à Guam pour la première fois en 1944, a depuis lors envahi la quasi-totalité de l'île. Les deux espèces présentant des caractéristiques écologiques similaires, notamment en ce qui concerne le choix des gîtes, on a voulu étudier l'évolution de leurs populations en comparant leurs densités relatives à 20 ans d'intervalle.

En 1948/49, une prospection a permis de récolter *Ae. albopictus* 24 fois et *Ae. guamensis* 59 fois dans des gîtes naturels, 86 fois et 140 fois dans des gîtes artificiels. En 1970, les chiffres correspondants ont été de 88 et 51 (gîtes naturels) et de 118 et 18 (gîtes artificiels). Une comparaison portant sur le nombre d'individus de

chaque espèce identifiés lors des deux enquêtes a montré que dans les gîtes naturels, les proportions d'*Ae. albopictus* et d'*Ae. guamensis* étaient en 1948/49 de 37,0 et 63,0%; en 1970, elles étaient de 67,9 et 32,1%. Dans les gîtes artificiels, on a récolté en 1948/49 47,0% d'*Ae. albopictus* et 53,0% d'*Ae. guamensis*; en 1970, les chiffres correspondants ont été de 95,5 et 4,5%.

Il semble donc que durant la période considérée le rapport entre les populations des deux espèces ait été modifié: forte diminution de la densité d'*Ae. guamensis* et augmentation correspondante de la densité d'*Ae. albopictus* dans les gîtes artificiels, surtout aux abords des habitations, et, dans une mesure moindre, remplacement d'*Ae. guamensis* par *Ae. albopictus* dans de nombreux gîtes naturels. L'éviction d'*Ae. guamensis* est peut-être due à des facteurs de milieu non identifiés, mais elle peut aussi résulter d'une concurrence entre deux espèces homologues du point de vue écologique, *Ae. albopictus* affirmant sa suprématie.

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