

# Temporal variation in genetic structure of a colonising species: *Aedes albopictus* in the United States

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The medically important mosquito, *Aedes albopictus*, has recently become established in several locations within the United States. A three-year survey of temporal variation in allele frequencies at ten enzymatic loci in 17 populations was undertaken to determine the extent and direction of change since the colonisation event. Significant, but non-directional, changes were detected in allele frequencies at most of the loci in all populations. Some alleles detected at low frequencies in earlier samples were not found in subsequent samples. Variance of allele frequencies remained unchanged. In at least two locations, there was an increase in mean heterozygosity, perhaps because of gene flow. There was no significant change in the levels of genetic variation within and among populations. The results from this study indicate that the breeding structure of *Ae. albopictus* in the U.S. did not differ substantially from that in a native habitat, either soon after colonisation or after several generations in the new habitat. We suggest that a large founder population, gene flow and a rapid population expansion could explain the present breeding structure of *Ae. albopictus*.

## INTRODUCTION

We have been studying the population genetics of *Aedes albopictus* (Skuse) (Diptera: Culicidae), a medically important mosquito, since its introduction into the U.S. in the early 1980s (Black *et al.*, 1988*a, b*, 1989). *Ae. albopictus* has historically been a successful coloniser (see Hawley 1988). Although there have been a few small introductions into the U.S. in the last few years (Eads, 1972; Reiter and Darsie, 1984), a large breeding population was discovered for the first time in Harris County, Texas, in August 1985 (Sprenger and Wuithiranyagool, 1986). The mosquito was probably introduced as eggs or larvae in used tyres shipped from Asia (Craven *et al.* 1987); diapause profiles and allozyme analysis suggest northern Japan as their most likely origin (Hawley *et al.*, 1987; Kambhampati *et al.*, in preparation). The present distribution of *Ae. albopictus* in the U.S. includes some 20 southeastern, north-eastern and midwestern states (Centers for Disease Control, 1987).

Previous studies on *Ae. albopictus* (Black *et al.* 1988*a, b*) from the U.S. and southeast Asia revealed that genetic drift at the local level is integral to its natural breeding structure. That is, in both habitats, most of the variation in allele frequencies arises from the within population component and the high variance within populations in the U.S. is not a consequence of the recent colonisation. Mean heterozygosity of U.S. populations was also comparable to that in one native habitat, suggesting the possibility of an unusually large founder population.

Given this information, we wished to determine the extent and the direction of change in allele frequencies of the U.S. populations of *Ae. albopictus* since the first sampling in 1986. Spatial and temporal variation in allele frequencies of 17 populations was studied over three years to determine if there was a change in local breeding structure and/or in the levels of genetic variation since the colonization. If genetic drift at the local level is still continuing, a large proportion of the variance in allele frequencies would be attributable to variation among locations within cities as reported by Black *et al.* (1988*a*). If there were "founder effects" (Mayr, 1963) directly associated with the colonisation, there might be a decrease over time in within

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population genetic variation and a concurrent increase in between population genetic variation through a random loss or fixation of alleles.

We undertook a nested spatial sampling of populations (Black *et al.*, 1988*a, b*, 1989) which involved sampling a number of cities and several locations within some of those cities. This design may enable one to detect drift at the local level by the partitioning of variance in allele frequencies into two components, among locations within cities and among cities. Random loss or fixation of alleles among the U.S. populations as a whole can be detected by estimating measures of within and between population variation, *i.e.*, mean expected heterozygosity and genetic distances, respectively.

Studies of genetic structure of colonising species often suggest a decrease in genetic variation resulting from drift, but only in populations several hundred generations removed from the original founders (*e.g.*, Bryant *et al.*, 1981; Easta, 1988; Johnson, 1988; Schwaegerle and Schaal, 1979; Taylor and Gorman, 1975). The discovery of *Ae. albopictus* soon after its arrival to the U.S. gives an opportunity to study the genetics of this species during the process of colonisation and to obtain a better understanding of the relative importance of the various evolutionary mechanisms in speciation and in the biological control of insect pests, which often involves the deliberate introduction of exotic species.

## MATERIALS AND METHODS

Samples of *Ae. albopictus* were collected twice a year in and around Harris County, Texas. *Ae. albopictus* was first reported in large numbers from a location within Harris County (Sprenger and Wuithiranyagool, 1986). Samples were collected once in late June/early July and again in late September/early October of the same year between 1986 and 1988. The number of sites sampled in Texas ranged from eight to 12. To obtain a measure of change in allele frequencies of US populations outside Texas, samples were collected in five different sites in the southeast, once in the summer of 1986 and again in the summer of 1988. These sites included three locations within the city of New Orleans, Louisiana, and one each in Jacksonville, Florida and Memphis, Tennessee (fig. 1 and table 1).

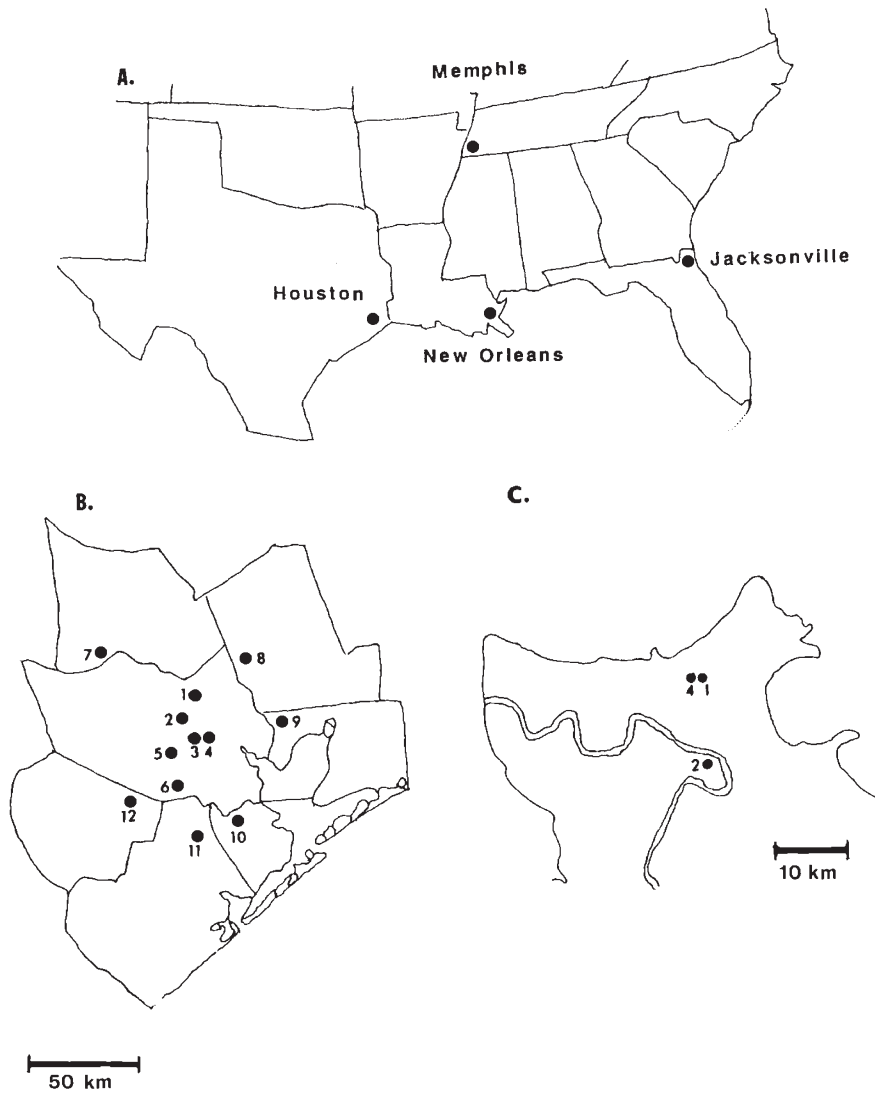
Eggs were collected in the field and were reared to adulthood (parentals) in an insectary at  $27 \pm 1^\circ\text{C}$  80 per cent RH and 12h L:12h D diel cycle. The number of larvae hatched from each location ranged from about 50 to a few hundred. Individuals assayed in 1986 consisted of the parentals. In subsequent assays, the parentals were allowed to mate and oviposit freely in a large cage and the F<sub>1</sub> adults were assayed.

Ten polymorphic loci were resolved for each population and sampling date using the Hoeffer SE600 vertical polyacrylamide gel electrophoresis

**Table 1** Location and dates at which *Aedes albopictus* samples were collected in Texas and elsewhere in the United States. + indicates that a sample was obtained and - indicates that a sample could not be obtained

Location	Sampling date				
	Summer 86	Summer 87	Fall 87	Summer 88	Fall 88
Texas					
Chambers	+	-	+	+	+
Galveston	+	+	+	+	+
Liberty	+	+	+	+	+
Brazoria	-	+	+	+	+
Fort Bend	-	+	+	+	+
Montgomery	-	-	+	+	+
Area 32	+	+	-	+	+
Area 34	+	+	-	+	+
Area 61	+	+	+	+	-
Area 203	+	+	+	+	+
Area 218	+	+	+	+	+
Area 509	+	+	+	+	+
New Orleans site 1	+	-	-	+	-
New Orleans site 2	+	-	-	+	-
New Orleans site 4	+	-	-	+	-
Memphis	+	-	-	+	-
Jacksonville	+	-	-	+	-

Summer = late June/early July, Fall = late September/early October.



**Figure 1** (A) A map of the southern United States showing the four cities in which populations of *Aedes albopictus* were sampled. (B) Sampling sites in around Harris county, Texas. 1: Area 218, 2: Area 203, 3: Area 32, 4: Area 34, 5: Area 61, 6: Area 509 (all Houston locations), 7: Montgomery county, 8: Liberty county, 9: Chambers county, 10: Galveston county, 11: Brazoria county, 12: Fort Bend county. (C) Sampling sites in the city of New Orleans. 1: New Orleans site 1 (North site), 2: New Orleans site 2 (Algiers) 4: New Orleans site 4 (Northwest site).

system. The Tris-citrate (TC) buffer system (0.78 M Tris, 0.24 M monohydrate citric acid, pH 7.2) was used to resolve aconitase (ACON),  $\alpha$ -glycerophosphate dehydrogenase ( $\alpha$ -GPDH), hydroxyl acid dehydrogenase (HAD), Isocitrate dehydrogenase (IDH) and malic acid dehydrogenase (MDH) and the Tris-boric acid-EDTA (TBE) buffer system (0.81 M Tris, 0.20 M boric acid, 15 mM EDTA disodium salt, pH 8.9) was used for esterase (EST), Glutamate-oxaloacetate transaminase (GOT), 6-phosphogluconic acid dehydrogenase (6-PGDH),

phosphoglucoisomerase (PGI) and phosphoglucomutase (PGM). The alleles were scored with reference to the most common allele ( $r_f = 1.0$ ) from the Memphis, Tennessee population. Mosquitoes were ground in 40  $\mu$ l of grinding buffer (10 per cent sucrose, 0.01 per cent bromophenol blue, 1 per cent triton X-100 dissolved in TC electrode buffer diluted 1:5).

Allele frequencies and their spatial and temporal heterogeneity were analyzed using BIOSYS-1 (Swofford and Selander, 1981). Genetic variation

was compared within and among populations and over time using bivariate correlation analysis and one-way analysis of variance (ANOVA). Wright's (1978) *F*-statistics were used to partition the variance in allele frequencies into variance among cities and among locations within cities. The data for the 1986 samples have been published by Black *et al.* (1988a).

## RESULTS

Allele frequencies are available from the authors upon request. Two loci, *Got* and  $\alpha$ -*Gpdh*, were monomorphic in all the populations and were therefore not considered in the analysis.

A contingency  $\chi$ -square analysis of variation in allele frequencies of each population over time indicated a significant difference ( $P < 0.05$ ) for most of the loci. The allele frequencies at *Pgm*, *Had* and *Est* varied significantly over time in 11/12 Texas populations, *Acon* and *Idh* in 9/12 populations and *Pgd* and *Pgi* in 6/12 populations. The least variable locus in Texas populations was *Mdh*, which varied only in 4/12 populations. The frequencies of the common alleles remained fairly stable over time in virtually all the populations and the significant differences were due primarily to the presence or absence of rare alleles. Some alleles that were observed at very low frequencies in earlier samples were not detected in subsequent samples. These alleles included the *F* allele at *Pgm* locus and the *E* allele at *Mdh* locus in Chambers county, and the *G* allele at *Had* locus in Areas 32 and 34 in Houston.

The pattern of allele frequency variation in the five populations outside Texas was similar to that observed within Texas. Allele frequency at the MDH locus did not vary with time in any of the populations. Allele frequencies at the *Idh* and the *Pgi* loci did not vary significantly in 4/5 populations; those at *Acon* varied in 2/5 populations and at *Est* and *Had* in 4/5 populations. The sample from New Orleans site 1, which was polymorphic for *Idh* in 1986, was found to be monomorphic in 1988. As in the Texas populations, there was no observable systematic change in the frequency of alleles at any of the loci studied. Alleles possibly lost include the *F* allele at *Had* locus in New Orleans sites 1 and 4, in addition to the *B* allele at *Idh* locus in New Orleans site 1 mentioned above.

Mean expected heterozygosity estimates for populations during the study period are given in table 2. One-way ANOVA was carried out on

average expected heterozygosity ( $H_{exp}$ , transformed to  $\arcsin\sqrt{H_{exp}}$ , Zar (1984)) for each population over all the sampling dates. There were no significant differences in mean heterozygosity in all comparisons of all populations. Although many of the correlations between sampling date and mean heterozygosity, mean number of alleles and per cent of loci polymorphic were negative, none were statistically significant at the 5 per cent level. Mean expected heterozygosity compared by ANOVA among all populations gave no differences significant at the 5 per cent level. Mean genetic distance (Nei's unbiased (Nei 1978) averaged over all the populations for each of the 5 sampling dates, table 3) did not indicate a systematic increase or decrease in divergence levels during the period of study.

The variance in allele frequencies was partitioned into variance among cities and among locations within cities for samples collected in the summer of 1986 and in the fall of 1988 (table 4). As previously reported by Black *et al.* (1988a, b), most of the variation at both sampling dates was attributable to variation within locations and only a small proportion of the total to variation among locations. In the summer of 1986, 86.3 per cent of the total variation was attributable to variance among locations within cities, and the remaining 13.7 per cent to variance among cities. In the fall of 1988, the corresponding figures were 85.6 and 14.4 per cent, respectively.

## DISCUSSION

In this paper, we presented the results of a three-year study on temporal and spatial variation in population genetic structure of *Ae. albopictus*, a recent arrival to the continental U.S. Our primary objective was to determine if we could detect in *Ae. albopictus* all or some of the consequences of drift often claimed to be associated with colonisation by a small number of individuals (*e.g.*, Mayr, 1963). Although decreased genetic variation has been demonstrated in some colonising species (*e.g.*, Bryant *et al.*, 1981; Easteal, 1988; Johnson, 1988; Schwaegerle and Schaal, 1979), it is not known how early after the colonisation event the effects of drift might be detectable and if such effects are a necessary consequence of colonisation.

Allele frequencies in the U.S. populations of *Ae. albopictus* changed significantly, albeit seemingly randomly, during the study period. Drift at the local level (Black *et al.*, 1988a), is probably

**Table 2** Estimates of mean expected heterozygosity for *Aedes albopictus* at each of the sampling dates. The mean sample size per locus is given immediately above the estimate

Location	Mean expected heterozygosity ( $\bar{x} \pm \text{S.E.M.}$ )				
	S 86	S 87	F 87	S 88	F 88
Brazoria	— 38	38 0.271 ± 0.063	14 0.283 ± 0.101	38 0.314 ± 0.101	38 0.340 ± 0.073
Chambers	0.321 ± 0.056 30	— 37	0.286 ± 0.084 37	0.271 ± 0.083 40	0.327 ± 0.086 40
Galveston	0.328 ± 0.081	0.347 ± 0.097 50	0.271 ± 0.082 15	0.234 ± 0.077 39	0.286 ± 0.086 38
Fort Bend	— 11	0.388 ± 0.089 40	0.299 ± 0.105 39	0.316 ± 0.103 39	0.324 ± 0.076 39
Liberty	0.292 ± 0.030	0.353 ± 0.090	0.266 ± 0.097 26	0.333 ± 0.089 39	0.282 ± 0.070 39
Montgomery	— 42	— 32	0.309 ± 0.103	0.287 ± 0.094 39	0.352 ± 0.090 40
Area 32	0.274 ± 0.090 42	0.314 ± 0.104 32	—	0.270 ± 0.091 39	0.265 ± 0.085 38
Area 34	0.274 ± 0.090 38	0.310 ± 0.106 44	— 39	0.332 ± 0.092 39	0.303 ± 0.076
Area 61	0.380 ± 0.101 37	0.273 ± 0.095 39	0.273 ± 0.082 18	0.314 ± 0.095 38	— 40
Area 203	0.362 ± 0.105 25	0.346 ± 0.102 38	0.276 ± 0.102 21	0.260 ± 0.092 38	0.222 ± 0.079 40
Area 218	0.349 ± 0.099 10	0.274 ± 0.080 37	0.310 ± 0.094 20	0.245 ± 0.094 35	0.256 ± 0.072 40
Area 509	0.296 ± 0.078 22	0.282 ± 0.091	0.276 ± 0.092	0.277 ± 0.099 38	0.248 ± 0.099
New OrL. 1	0.354 ± 0.089 19	—	—	0.162 ± 0.070 38	—
New OrL. 2	0.224 ± 0.083 22	—	—	0.207 ± 0.060 39	—
New OrL. 4	0.274 ± 0.069 16	—	—	0.269 ± 0.084 38	—
Jacksonville	0.211 ± 0.089 45	—	—	0.352 ± 0.093 40	—
Memphis	0.122 ± 0.069	—	—	0.280 ± 0.080	—

Abbreviations: S 86: Summer 86; S 87: Summer 87; F 87: Fall 87; S 88: Summer 88; F 88: Fall 88.

**Table 3** Temporal change in mean genetic distance (Nei's unbiased) in US and Texas populations of *Aedes albopictus*. The genetic distances among all populations at a given sampling date were averaged to obtain the values shown. *n* represents the number of values in the genetic distance matrix

Sampling date	<i>n</i>	Mean genetic distance ( $\pm \text{S.E.M.}$ )
Texas		
Summer 1986	28	0.030 ± 0.004
Summer 1987	45	0.042 ± 0.004
Fall 1987	45	0.036 ± 0.004
Summer 1988	66	0.056 ± 0.004
Fall 1988	55	0.029 ± 0.004
United States		
Summer 1986	10	0.109 ± 0.020
Summer 1988	10	0.112 ± 0.012

continuing. Some of the alleles detected at low frequencies in 1986 were not detected in subsequent samples, suggesting loss through genetic sampling. For example, in New Orleans site 1, the *Idh* locus, which was polymorphic in all the populations examined (including New Orleans site 1 in 1986), became monomorphic in a few generations. Control efforts involving insecticides in some parts of the U.S. may also have contributed to the loss of some low frequency alleles. Selection as the causal factor is unlikely because of the short time involved and the lack of a systematic change in allele frequencies at the *Idh* locus in any of the other populations. Despite the loss of some low frequency alleles, there was no significant overall change in mean heterozygosity over the three-year period; none of the correlations between time and

**Table 4** The variance of allele frequencies of *Aedes albopictus* partitioned into variance among locations within cities and among cities. Variance components were combined among all loci. See text for further details

Sampling date	Source	Variance component	Per cent of total
Summer 1986	Within locations	0.241	86.7
	Among cities	0.037	13.3
	Total	0.278	
Summer 1988*	Within locations	0.308	85.6
	Among cities	0.053	14.4
	Total	0.361	

\* Includes Texas samples from the fall of 1988 and the U.S. samples from the summer of 1988

the various measures of genetic variation were statistically significant, indicating that genetic variation is being maintained within populations.

In addition, there was no significant change in variance of allele frequencies among locations within cities or among cities over the three-year period. In 1986, the variance component for among locations within cities was 86.7 per cent and in 1988, 85.6 per cent. Black *et al.*, (1988*b*) found that variance among locations within regions in Malaysia and Borneo was 79.3 per cent. The variance of allele frequencies among locations within cities in each case is about 4–5 times greater than that among cities. Although we did not partition the variance at each of the five sampling dates for the Texas populations, the lack of a systematic change in the divergence levels among these populations (table 3) suggests that there was no change in the variance of allele frequencies over time (Falconer, 1981). Therefore, with regard to variance components, the U.S. populations were similar to those from a native habitat soon after establishment and remained so after several generations in the new environment. Strong local differentiation also exists in the ribosomal DNA nontranscribed spacer region of *Ae. albopictus* (Black *et al.*, 1989).

Black *et al.* (1988*a, b*) suggested that local genetic drift could arise from a patchy distribution of breeding sites and dispersal habits of *Ae. albopictus*, which in the U.S. breeds primarily in tyre dumps in urban areas. Each dump may contain thousands of tyres and is usually separated from others by a considerable distance and urban structures creating barriers to dispersal. In very large tyre dumps, the population may be further subdivided because *Ae. albopictus* disperses only about 150–200 m from its breeding sites (Hawley, 1988).

Our results confirm those of Black *et al.* (1988*a, b*) that genetic drift is a characteristic of the local breeding structure of *Ae. albopictus*. We have also shown that breeding structure has not changed as a result of the colonisation. The lack of any “founder effects” (Mayr, 1963), other than the loss of some rare alleles, suggests several possibilities. For example, it could be too early to detect significant loss of within population genetic variation.

Direct and circumstantial evidence, however, suggests that the dynamics of colonisation of the U.S. by *Ae. albopictus* is a more likely explanation for the observed patterns of allele frequency variation. First, it is probable that there was one very large introduction and/or repeated introductions of *Ae. albopictus* into the U.S. The high levels genetic variation and the local breeding structure of the U.S. populations, both comparable to those in a native habitat (Black *et al.*, 1988*b*), support this view. Second, there was considerable movement of population within the U.S. subsequent to establishment in Houston with a rapid spread of *Ae. albopictus* to at least 20 states in about 4–5 years. Such movement must have resulted in considerable gene flow. For example, the  $H_{exp}$  for Memphis increased from 0.122 in 1986 to 0.280 in 1988 and for Jacksonville from 0.211 to 0.352. Third, a rough estimate of effective population sizes based on  $F_{st}$  values (Easteal, 1985) indicated an increase in the U.S. from the summer of 1986 through the fall of 1988. (The estimates for *Ae. albopictus* in Texas are: 102, 134, 155, 134 and 260 for each of the five sampling dates, respectively. We assumed that: *Ae. albopictus* goes through ten generations per year, twenty generations have elapsed in the U.S. before the first sampling and five generations elapsed between sampling in the summer and the sampling in the fall of each year). This suggests that *Ae. albopictus* population is expanding, perhaps aided by an influx of new genetic material from locations within the U.S. A large founder population, gene flow and a rapid increase in population size may impede the loss of genetic variation during founder events (Falconer, 1981; Janson, 1987; Nei *et al.*, 1975).

Our results indicate that *Ae. albopictus* was introduced into the U.S. with most of the genetic variation intact. This may have substantially enhanced its chances for establishment. The large founder population and rapid increase in population size also suggest that a future loss of genetic variation, as a direct consequence of the colonisation event, is unlikely.

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