

COMPARISON OF REPRODUCTIVE POTENTIALS OF *Aedes* (*Stegomyia*) *albopictus* Skuse and *Aedes* (*Stegomyia*) *polynesiensis* Marks¹

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Interspecific competition appears to be an important factor in determining the distribution and abundance of animals. The principle should apply also to mosquitoes, and so is of interest especially when two species with similar ecological requirements become sympatric in some parts of their geographic ranges. It has been suggested that *Aedes aegypti* and *A. albopictus* have exhibited the phenomenon of competitive displacement in certain areas of southeast Asia (Gilotra *et al.*, 1967). Two other potential competitors are *A. albopictus* and *A. polynesiensis*.

Gubler (1969a, 1969b) has shown that *A. albopictus* rapidly displaces *A. polynesiensis* from mixed species competition cages and suggested that this rapid elimination was primarily due to cross-insemination sterility of the female *A. polynesiensis* by *A. albopictus* males. However, according to De Bach (1966), a slight advantage in reproductive potential would be all that is needed for one species to eliminate another species from a common niche. This investigation was a part of a more complete study on competitive displacement between *A. albopictus* and *A. polynesiensis*, and was designed to determine whether one species has a reproductive advantage over the other.

MATERIALS AND METHODS

For observations on fecundity and adult longevity, adults were kept in gallon-sized cardboard cylinders, covered at the upper end with mosquito netting, or cubic foot aluminum screen mesh cages.

At the beginning of each experiment, 25 male and 25 female pupae of each species were placed in their respective cages. Starting 1 day after emergence, the females were offered human blood meals daily until all had fed. Subsequent blood meals were offered after each oviposition. A maintenance diet consisted of 10 percent sucrose solution. The cages were checked daily for eggs and dead mosquitoes. All of these mosquitoes were held in incubators or in an air conditioned insectary at 25–26° C. and 75–80 percent R. H.

In experiments on the effect of relative humidity on longevity, 25 males and 25 females were allowed to emerge in the cardboard cylinder cages and were fed only a 10 percent sucrose solution. They were held in incubators at a constant temperature of 25° C. Relative humidities ranging from 27 to 85 percent were controlled by appropriate amounts of CaSO₄ (Drierite).

Egg viability was studied by placing newly emerged females in cubic foot cages with twice as many males to insure insemination. A blood meal was offered 4 days after emergence and an oviposition trap was provided on the evening of the eighth day. On the following morning, the paper lining the trap was removed, placed under a low power microscope for the purpose of counting the eggs, and then cut into strips, each with 1000 eggs. Thus

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the eggs were less than 16 hours old at the beginning of each experiment. Deoxygenated water was utilized as a hatching stimulus for the first 24 hours, after which the egg papers were transferred to regular tap water for the remainder of the experimental period. The pans were examined daily for newly hatched larvae, which were removed and counted.

EXPERIMENTAL RESULTS

FECONDITY. The object of these experiments was to compare the egg production of the two species. An adult male and female of each species were isolated in pint cardboard cartons and provided with blood and 10 percent sucrose solution. Unfortunately, most of the *A. albopictus* females refused to take blood in these small cartons and those that did so laid only a few eggs. Therefore, the number of eggs per cycle, and the number of days between cycles were not determined for individual *A. albopictus* females. *A. polynesiensis* females, on the other hand, fed and oviposited freely in these containers and the results showed that the first 3 gonotrophic cycles were the most productive. The mean numbers of eggs were 86.5, 91.9, and 64.4 for cycles 1, 2, and 3 respectively, and of all the eggs produced by a female, 84.6 percent were deposited, on the average, in these cycles. Thus, with increasing age,

the number of eggs per blood meal decreased while the number of days between gonotrophic cycles increased.

In an attempt to obtain normal gonotrophic activity in *A. albopictus*, the small containers were replaced with gallon cardboard cartons, provided with a sleeve and bobbinet top, and with cubic foot aluminum wire cages. The eggs were collected and counted for as long as the females remained alive. Because the gonotrophic cycles of the mosquitoes in these cages were not rhythmic, the number of eggs per cycle and the number of days between cycles again could not be calculated. The total mean number of eggs laid by a female in her lifetime was calculated for each type of cage and presented for comparison in Table 1. *A. albopictus* was less adapted to small confined areas, as suggested by the increased number of eggs laid with each increase in cage size. The cubic foot cages, with a mean of 370.5 and a maximum of 412.0 eggs per female, were the most favorable. *A. polynesiensis* females, on the other hand, laid more eggs (average of 386.1) when held in the smaller gallon container than in the cubic foot cage (average of 167.0). Thus it appears that the total egg-laying capacity of these two species is nearly identical under conditions most favorable to the species.

Since the gonotrophic activity of *A. albopictus* could not be observed on an

TABLE 1.—The effect of cage size on fecundity of *A. albopictus* and *A. polynesiensis*.

Species	Replicate No.	No. Females	Numbers of Eggs Per Female*			
			Pint Carton	Gallon Carton	Cubic ft. Cage	Total Average Egg/♀
<i>A. albopictus</i>	1	50	302.0	329.0	315.5
	2	50	276.0	412.0	344.0
	mean		289.0	370.5	329.8
<i>A. polynesiensis</i>	1	69	263.5	435.6	149.0	292.3
	2	50	336.6	185.0	260.8
	mean		263.5	386.1	167.0	276.5

* Mean of 25 females/container/replication.

individual basis, the number of eggs per cycle was not determined. However, a very good estimate of the number of eggs produced in the first cycle was obtained from a series of experiments on oviposition preferences (Gubler, 1969b). A total of 1140 *A. albopictus* females laid 71,121 eggs or an average of 62.4 per female. The same number of *A. polynesiensis* females produced 72,718 eggs, or an average of 63.8 per female. The numbers of eggs produced following engorgement on four different hosts are given in Table 2. Both

hatched larvae were counted until a total of 11 days had elapsed from the time of oviposition. The results, presented in Table 3, show that whereas *A. albopictus* eggs were unaffected by direct or early immersion in water, *A. polynesiensis* eggs survived better if matured for 3 or 4 days prior to immersion. Although maturation apparently continues during early immersion in water, hatching was delayed by a day or two in both species, possibly as a result of the temperature difference between air and water.

TABLE 2.—The effect of blood from four different hosts on the number of eggs laid by *A. albopictus* and *A. polynesiensis* females.

<i>A. albopictus</i>					
Host	Guinea Pig	Rat	Mouse	Chick	Totals
No. females	50	50	50	50	200
No. fed	46	48	30	32	156
% fed	92	96	60	64	
No. eggs	3004	2597	2155	1615	9413
No. eggs/♀	65.3	54.1	71.8	51.8	
<i>A. polynesiensis</i>					
No. females	50	50	50	50	200
No. fed	34	30	15	26	105
% fed	68	60	30	52	
No. eggs	2956	2737	1698	1978	9369
No. eggs/♀	86.9	91.2	113.2	76.1	

species produced more eggs on mouse blood, although this host was less attractive than guinea pigs or rats in terms of feeding response. Females of *A. polynesiensis* produced a larger number of eggs per batch than did those of *A. albopictus*, but the total egg production was about the same.

EGG VIABILITY. The purpose of these experiments was to make direct comparisons of viability and survival of the eggs of *A. albopictus* and *A. polynesiensis*. In the first experiment, strips of paper containing eggs less than 16 hours old were placed directly in deoxygenated water. Other strips containing eggs from the same batch were incubated in moist chambers for 2, 3 and 4 days before immersion. The

To test the effect of desiccation on egg survival, strips of 1000 eggs were matured (i.e., incubated in a moist chamber) for 4 days, then placed in a loosely capped plastic container and stored at 24 to 25° C. and 70–75 percent R. H. for 4 days,

TABLE 3.—Egg survival after various periods of maturation.

Days of maturation	Percent of Eggs Hatching				
	0	1	2	3	4
Days of immersion	11	10	9	8	7
<i>A. albopictus</i>	60.3	44.4	54.0	67.1
<i>A. polynesiensis</i>	34.3	41.7	52.9	54.3

TABLE 4.—The effect of desiccation on egg survival.

Observation No.	Percent of 1,000 Eggs Hatched									
	1			2			3			
Desiccation period Days in water	4 days 300	1 week 300	Control 77	2 weeks 75	1 month 250	2 months 250	Control 75	3 months 250	Control 75	Control 75
<i>A. albopictus</i>	74.6	77.9	76.8	30.0	43.8	39.9	59.4	49.3	67.1	
<i>A. polynesiensis</i>	55.4	63.7	79.0	15.3	11.5	2.0	44.7	15.1	54.3	

1 week, 2 weeks, and 1, 2, and 3 months. After the respective periods of desiccation, the eggs were immersed in water continuously for periods up to 300 days. The control eggs were placed in water immediately after maturation. The results are presented in Table 4. A week of desiccation had no effect on the survival of *A. albopictus* eggs, and even after 3 months there was an increase in mortality of only about 20 percent (observation 3). The survival of *A. polynesiensis* eggs, on the other hand, was reduced by about 20 percent after drying for 4 days to 1 week, 30 percent after 2 weeks to a month, and 40 percent after 2 to 3 months.

All of the eggs used in the above experiment were placed in water and left there continuously after their respective treatments. The following experiment was designed to determine the consequence of alternate wetting and drying on survival. Following the 4-day maturation period, one group of eggs was immersed for 1 week and then dried for 1 week. Another group was first dried for 3 days and then immersed for 3 days. The control group, after maturation, was immersed in water continuously. These alternate periods of wetting and drying were continued for 250 days. The results, presented in Table 5, show that survival was comparable to

ing, the viability of *A. albopictus* eggs was reduced by only about 20 percent and that of *A. polynesiensis* eggs by about 40 percent. Thus it appears that a continuous initial period of desiccation is no more detrimental than alternate periods of drying and wetting.

The larvae hatching from the eggs in these experiments were counted every day and each pan was observed for 50 days following the last hatch. This made possible an estimate of the longevity of the embryos. Most of the eggs of both species hatched within 20 days of immersion in water with subsequent hatches occurring sporadically and in small numbers. However, a second peak of hatching of *A. albopictus* eggs occurred between 100 and 160 days and of *A. polynesiensis* eggs between 80 and 120 days. The maximum survival times were 243 days for *A. albopictus* and 218 days for *A. polynesiensis*.

ADULT LONGEVITY. The effect of relative humidity on adult survival was determined by placing the gallon sized cages containing the newly emerged adults in three incubators controlled at 25° C. and 27, 55, and 85 percent R. H. respectively. The cages containing *A. albopictus* and *A. polynesiensis* were placed side by side in each incubator. The results of two replications, presented in Table 6, show that the survival of *A. albopictus* females was greatly superior to that of *A. polynesiensis* at all three relative humidities. The LT₅₀ values suggest that the lower humidities were more favorable to *A. albopictus* females than were the higher humidities, although the LT₉₀ values suggest just the opposite. The maximum survival times for females of this species were nearly identical at the highest and lowest humidities. Thus it appears that the R. H. in the range tested did not significantly affect the survival of *A. albopictus*. On the other hand, the survival of *A. polynesiensis* adults was very low at 27 percent R. H., but was enhanced with increasing humidity.

The mosquitoes in the above experiment were given only a maintenance diet of

TABLE 5.—The effect of alternate wetting and drying on egg survival.

Treatment of eggs	Percent of 1,000 Eggs Hatched*		
	Control	Wet 1 week Dry 1 week	Dry 3 days Wet 3 days
<i>A. albopictus</i>	90.6	90.5	58.2
<i>A. polynesiensis</i>	68.3	70.7	22.0

* Total observation period of 250 days.

that of the controls if the eggs were immersed for 1 week before the first period of desiccation. However, if the eggs were dried for 3 days before immersion, survival of *A. albopictus* embryos was reduced by about 30 percent and that of *A. polynesiensis* by about 45 percent. As shown in Table 4, after 3 months of dry-

TABLE 6.—Survival of adult *A. albopictus* and *A. polynesiensis* at different relative humidities and 20° C.

% Relative Humidity	Survival in Days					
	<i>A. albopictus</i>					
	LT ₅₀		LT ₁₀		Maximum	
n=2	♂	♀	♂	♀	♂	♀
27±1.0	15.2	48.3	29.7	68.5	35	101
55±0.6	14.0	42.5	28.0	72.8	50	88
85±0.6	6.0	36.0	32.2	80.5	68	104
	<i>A. polynesiensis</i>					
27±1.0	8.5	11.0	15.0	20.5	21	22
55±0.6	11.5	19.5	19.0	33.0	24	44
85±0.6	16.5	23.5	28.5	36.5	42	48

10 percent sucrose solution. To determine whether diet affected longevity, another group of mosquitoes were observed under identical conditions, but were provided with blood immediately after emergence and subsequently after each oviposition throughout their life. The relative humidity was held at 80 percent. A comparison of the survival of this group of females with that of the sugar-fed mosquitoes held at 85 percent relative humidity (from Table 6) is presented in Table 7. The ability of females of both species to survive was greatly enhanced when provided with periodic blood meals. The LT₅₀ values of the blood-fed groups were nearly 2 times higher than those of the mosquitoes fed sugar water only.

In fecundity experiments, three types of cages were used. The data concerning the relative survival of the adults in these cages are summarized in Table 8. All of the females were provided with periodic

blood meals and were held at 25° C. and 80 percent R. H. Both *A. albopictus* and *A. polynesiensis* survived equally well in the pint and gallon containers, but both had a decreased survival time in the larger wire cages. This decreased longevity was more pronounced in the latter species. *A. albopictus* females had a longer survival time than *A. polynesiensis* females in all types of containers.

DISCUSSION

For competitive displacement to occur, direct attack on one species by the other is not necessary. In theory, an ecological niche can support a certain maximum population density. If two species are competing for this niche, the one with even a slight reproductive advantage should eventually become the sole inhabitant of that niche. This advantage would be provided by longer adult survival, greater fecundity, more resistant eggs and similar biological characteristics.

These laboratory studies have emphasized the superiority of *A. albopictus* over *A. polynesiensis* in all of the above aspects except the egg-laying capacity, which was about the same for both species. Both species preferred to feed on rats and guinea pigs rather than on mice, which were the least preferred of the four hosts and on whose blood the most eggs were produced. A similar finding has been reported for the highly anthropophilic *A. aegypti*,

TABLE 7.—The effect of blood on survival of adult females.

n=2	Survival in Days		
	LT ₅₀	LT ₁₀	Maximum
	<i>A. albopictus</i>		
Without blood	36.0	80.5	104
With blood	67.0	96.5	122
	<i>A. polynesiensis</i>		
Without blood	23.5	36.5	48
With blood	47.0	62.3	83

TABLE 8.—The effect of cage size on adult survival.

Type of cage	Survival in Days					
	LT ₅₀		LT ₉₀		Maximum	
	♂	♀	♂	♀	♂	♀
	<i>A. albopictus</i>					
Pint cardboard container	30.0	>65.0	50.0	59	...
Gallon cardboard container	14.0	67.0	35.0	96.5	59	122
Aluminum wire cage (1 cu. ft.)	12.0	55.5	24.5	79.0	35	86
	<i>A. polynesiensis</i>					
Pint cardboard container	18.0	40.0	33.0	60.0	39	65
Gallon cardboard container	14.5	47.0	34.5	62.3	39	83
Aluminum wire cage (1 cu. ft.)	12.5	21.0	28.7	40.5	36	45

which produced the largest number of eggs after a blood meal from the frog (Woke, 1937). Host preferences have been shown to be influenced by such factors as heat, moisture, and CO₂, which in turn are influenced by body size. Possibly the larger size of the guinea pig and rat was the most influential factor in attracting *A. albopictus* and *A. polynesiensis* females.

Eggs of *Aedes* mosquitoes remain in a state of suspended development until some hatching stimulus activates the embryo. This is an adaptation to their special breeding places which usually have fluctuating water levels. Thus eggs laid above the water line in tree holes, tins, pots, and the like often are exposed to extended periods of desiccation as the water evaporates. With the onset of rains, the water level rises and floods the eggs, stimulating them to hatch. Thus, it is apparent that egg survival is a very important factor in the survival of these species. The superiority of *A. albopictus* over *A. polynesiensis* in egg survival would give the former species a marked advantage.

It was observed that a majority of the eggs of both species placed in water hatched within the first 20 days. Subsequent hatching followed a sequence of alternating long periods of dormancy and

short periods of hatching. A similar phenomenon was observed with *A. polynesiensis* eggs by Buxton and Hopkins (1927), who suggested the possibility of some general hatching stimulus. If there is a common hatching stimulus, it should have affected all eggs at the same time. This was not the case. However, the long dormant periods that some of the eggs passed through indicates that there may be an embryonic biological clock which, through the evolutionary processes of selection and adaptation, has enhanced the ability of these mosquitoes to survive in their respective environments.

A. albopictus females were far superior to *A. polynesiensis* females in their ability to survive for extended periods under all of the conditions tested. An interesting aspect of these experiments was that *A. albopictus* females survived as long at low as they did at high relative humidities. Hylton (1965) reported similar results with this species and attributed it to an apparent higher degree of spiracular control and other mechanisms for regulating the intake or outflow of body moisture.

The data presented in this report clearly indicate that *A. albopictus* has a reproductive advantage over *A. polynesiensis*. However, in order to make a valid comparison, the net reproductive rates of the two

species must be considered, because the output of adults in a given generation is a function of the numbers in the preceding generation and the net reproductive rate. The gross reproductive rate (Rg) of mosquitoes is the total number of fertile eggs produced by the average female. The net reproductive rate (Rn) then would be the product of the gross rate, the sex ratio (S), and the probability of survival from egg to adult (P). Thus:

$$Rn = (Rg) (S) (P)$$

Complete fertilization and the usual sex ratio of normal eggs (0.5) must be assumed. From Table 1, the gross reproductive capacities for *A. albopictus* and *A. polynesiensis* under the most favorable conditions are taken as 370.5 and 386.1 eggs respectively. The probability of survival from egg to adult was found to be 0.49 and 0.44 for *A. albopictus* and *A. polynesiensis* respectively (Gubler, 1969) and therefore,

$$Rn_{\text{albo}} = (370.5) (0.5) (0.49) = 90.77$$

and

$$Rn_{\text{poly}} = (386.1) (0.5) (0.44) = 84.94$$

Thus every adult *A. albopictus* and *A. polynesiensis* female that emerged had the potential of giving rise to 90.77 and 84.94 adult females respectively. A stable population would have a net reproductive rate of 1.0. However, it should be remembered that these were laboratory populations grown under optimal conditions. None of the parasites, predators, diseases, or environmental catastrophes which plague natural populations are present, and therefore large values for the net reproductive rates are to be expected. The rates calculated above confirm that *A. albopictus* has a higher net reproductive potential and therefore would have the advantage if the two species were competitors for the same ecological niche.

ABSTRACT

Comparative studies on the reproductive potential of *Aedes (Stegomyia) albopictus* and *A. (S.) polynesiensis* were run as a part of a more complete study to deter-

mine whether the competitive displacement principle applies to these species under laboratory conditions. It was found that under the most favorable conditions for each species the fecundity of *A. polynesiensis* and *A. albopictus* was nearly identical, both in terms of the total eggs produced during their life time and the number of eggs in the first gonotrophic cycle. Both species preferred to feed on guinea pigs or rats, but produced the most eggs when fed on mouse blood.

The eggs of *A. albopictus* were clearly more resistant to desiccation than those of *A. polynesiensis* and were superior in their ability to survive under all conditions tested. Although the majority of eggs of both species hatched within the first 20 days, both exhibited a second peak of hatching after a period of dormancy.

A. albopictus females were longer lived than *A. polynesiensis* females and were better adapted to survive under all of the conditions tested.

The reproductive advantage enjoyed by *A. albopictus* as a result of its higher egg and adult survival was confirmed by calculating net reproductive rates for the two species. It was concluded that, on the basis of reproductive potential, *A. albopictus* would be the superior competitor if the two were brought together.

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CONVERSION OF THERMAL FOGGERS FOR ULV APPLICATION

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Mount *et al.* (1968) reported on the effectiveness of non-thermal, ultra-low volume (ULV) aerosols applied by ground equipment. Further work by Mount *et al.* (1970) demonstrated that the Leco ULV aerosol nozzle will produce a cold aerosol at least as effective as thermal aerosols at air pressures attainable from a converted Leco 120 fog machine.

This paper deals with practical aspects of converting thermal foggers to operate as ULV aerosol generators. In essence the conversion amounts to removing all parts from a machine except the engine and blower and installing an insecticide system and the Leco nozzle.

The first consideration in converting a machine is whether the engine-blower combination has enough air output to produce sufficiently small droplets with the Leco nozzle. This is important operationally since droplets larger than 25 μ will impinge readily on stationary objects

reducing the efficiency of the spray and, with insecticides currently in use, possibly damage automobile finishes.

Mount *et al.* (1970) reported on droplet sizes produced by the Leco nozzle at 3.5 psi air pressure. Using the general methods employed by them, further tests were conducted to determine the lowest practical operating pressure for the nozzle. These data are summarized in Table 1. From this table it can be seen that pressures lower than 3.0 psi produce excessively large droplets and operation at lower pressures is not recommended. In practice, the authors operated converted units routinely for one season at 3.0 and 3.5 psi with no reported cases of automobile or vegetation damage and with a higher degree of mosquito control than ever attained with thermal fogging as indicated by daily routine landing rate counts.

Figure 1 shows the air deliveries required to maintain pressures up to 13 psi in the Leco nozzle. These values were determined with a nozzle attached to a Roots-Connersville Model 74 RAI blower

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