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Genetic-control trials and the ecology of *Aedes aegypti* at the Kenya coast

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Abstract

This review summarizes results of field trials for the genetic control of *Aedes aegypti* conducted in coastal Kenyan villages in 1974-75. Two separate releases, in dry and wet seasons, of translocation-heterozygote males induced 60-70% sterility in offspring of native *Ae. aegypti* but did not reduce adult-mosquito population sizes in the release villages because of density-dependent larval mortality. A translocation homozygote, released for population replacement, failed to colonize village environments because of inferior fitness characteristics, including an aversion for ovipositing in clay water pots, the primary indoor breeding container used by native *Ae. aegypti.* The Mosquito Biology Unit of ICIPE, spawned by these genetic-control experiments, contributed a rich harvest of information on the ecology, genetics, and behaviour of coastal Kenyan mosquitoes, particularly *Ae. aegypti*. Some examples cited here are the differences that separate sympatric feral and domestic populations of this species in this region of Kenya and the regulation of adult population sizes of indoor *Ae. aegypti* by larval food resources and human behaviour.

Keywords: *Aedes aegypti*; density dependence; fitness; genetic control; Kenya; translocations

Introduction

A surge in research on vector genetics in the 1950s and 60s spearheaded interest in applying this growing knowledge to vector control (Wright and Pal 1967). Among the genetic-control mechanisms proposed was the introduction of chromosome translocations into natural populations of vector species (Pal and LaChance 1974). In females heterozygous for induced translocations, these chromosome rearrangements cause various levels of infertility (Robinson 1976), which, at least on theoretical grounds, can be perpetuated into subsequent generations. Individuals carrying two different types of translocations (double heterozygotes) are expected to introduce proportionately more sterility (Uppal, Curtis and Rai 1974). Preliminary results from India and Florida, USA suggested that some translocation heterozygote males of *Aedes aegypti* (L.) mated competitively with wild females after field releases (Grover et al. 1976; Seawright et al. 1976).

An alternative use of chromosome rearrangements was proposed for driving desirable genes, such as refractoriness for pathogens, into vector populations through

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releases of translocation homozygotes (Curtis 1968). In principle, population replacement is facilitated by matings between native vectors and released homozygotes, which then yield semisterile, translocation-heterozygote offspring (Curtis 1968; Lorimer, Lounibos and Petersen 1976).

Field trials were conducted in the 1960s and 70s for genetic control of *Aedes*, *Anopheles* and *Culex* mosquitoes, among which were projects in India, the USA and Kenya where translocated mosquitoes were released. In the early 1970s the coast of Kenya was selected as a field site for genetic-control trials on *Ae. aegypti* because of (a) year-round breeding of this species in discrete and experimentally tractable villages; (b) affiliation with, and support from, the recently established International Centre of Insect Physiology and Ecology (ICIPE) in Nairobi; (c) major funding to test the feasibility of genetic control from USAID to G.B. Craig, Jr., University of Notre Dame, a member of the ICIPE advisory board. The Mosquito Biology Unit (MBU – also the Kiswahili word for 'mosquito') of ICIPE, later renamed the Coastal Research Station, was established in 1971 and headquartered in a colonial beach estate north of Mombasa island.

Chromosomal Translocations and Sterility

A translocation is a chromosomal rearrangement resulting from the simultaneous breakage of two non-homologous chromosomes and the subsequent interchange of the broken segments. Translocations can be induced in insects by irradiation and maintained by crosses to appropriate marker stocks. Among wild *Ae. aegypti* females mated to released males bearing translocations, the incidence of sterility was measured as the proportion of non-hatching eggs. For experiments conducted in Kenya, matings to single translocation heterozygote males yielded 50% infertile eggs and matings to double translocation heterozygotes produced approximately 75% non-hatching eggs (McDonald, Häusermann and Lorimer 1977; Petersen, Lounibos and Lorimer 1977).

Preliminary site and mosquito population characteristics

The choice of the Kenya coast was influenced by the relatively comprehensive knowledge of local mosquito natural history accrued by colonial entomologists (e.g. Teesdale 1959; Van Someren, Teesdale and Furlong 1955; Van Someren, Heisch and Furlong 1958). *Aedes aegypti* in this region was already known to be composed of two, morphologically distinguishable forms, the more anthropophilic of which was found predominantly indoors in human dwellings (McClelland 1960; Van Someren, Teesdale and Furlong 1955).

The Rabai area, approximately 25 km west of Mombasa, was chosen as an experimental site because of (a) easy accessibility from Mombasa; (b) year-round larval habitat for domestic *Ae. aegypti*, typically in clay jars maintained indoors for water storage; (c) compact villages of 15-40 houses, often separated by 0.5-2.0 km, which could be regarded as experimental units; (d) the hospitality of the Warabai people, one of the mijikenda (nine tribes) of the Kenya coast (Spear 1978).

The Rabai area is situated on a coastal plain of porous, sandy soil, with a peridomestic vegetation dominated by coconut palms and an understorey of scattered mango, cashew, and citrus trees. Small patches of indigenous forest were protected

from destruction by their religious significance or by their occurrence on the steep embankments of the Kombeni River. Considerable brush and scrub had been cleared for cultivation of crops such as maize, beans, and sweet potatoes. The climate of the region is influenced by SE and NE monsoons, which typically promote two annual rainy periods, the wetter usually in April-May and the other in November-December.

Prior to releases of translocated mosquitoes, estimates of adult population sizes of *Ae. aegypti* in villages of 26-34 houses were made by applying Bailey's, Jolly's and Lincoln's methods to mark-recapture data. Results from independent estimates in seven different villages yielded adult numbers ranging from 635 to 1200 individuals (Lorimer, Lounibos and Petersen 1976; McDonald, Häusermann and Lorimer 1977; Petersen, Lounibos and Lorimer 1977).

Dispersal of adult *Ae. aegypti* in the peridomestic environment was also investigated by mark recapture. When released outside a village, recaptures within the village dropped off markedly beyond 200 m away from the village complex (McDonald 1977b). Within a village, most dispersal occurred within 20 m of the release house and was independent of mosquito age (McDonald 1977b). Most *Ae. aegypti* were recaptured in only one or two houses, but a few visited as many as five (Trpis and Häusermann 1986). Independent estimates of daily survivorship were 0.83 and 0.89 for females and 0.69 and 0.77 for males (McDonald 1977a; Trpis and Häusermann 1986).

The seasonal stability of the indoor form, *Ae. aegypti aegypti*, contrasted sharply with the episodic appearance of the feral *Ae. aegypti formosus* after rainfalls (Lounibos 1981; Trpis and Häusermann 1986). House-entering propensity was shown to be a characteristic of the indoor form (Trpis and Häusermann 1975) and genetically determined (Trpis and Häusermann 1978). These authors proposed that peridomestic samples of *Ae. aegypti* represented rainy-season hybridization between feral and domestic forms (Trpis and Häusermann 1978), but they did not rule out that these samples were composed of mixtures of these forms.

Production and releases of translocated *Ae. aegypti*

Three independent releases of translocation heterozygotes and a homozygote were conducted between early 1974 and mid-1975 (see Table 1). The first release was composed of a mixture of single and double translocation-heterozygote males produced by irradiation of *Ae. aegypti* from the Rabai area (McDonald, Häusermann and Lorimer 1977). The average fertility of released males mated with caged Rabai females was 37%.

A mean of 814 translocated males was released daily for 10 weeks during the dry season into Chibarani (CHI) village, whose native *Ae. aegypti* population was estimated to be 635 adults (McDonald, Häusermann and Lorimer 1977). Although the fertility of eggs collected towards the end of the release period decreased to below 40%, after the cessation of releases the egg hatching capacity increased rapidly, and there was no evidence for a reduction in adult population size of domestic *Ae. aegypti* in CHI. McDonald, Häusermann and Lorimer (1977) suggested that density-dependent larval mortality in breeding containers buffered the productivity of adults from any measurable effect of the temporary reduction in fertility. Despite the rapid rebound of the mosquito population in CHI to normal fertility, genetic markers linked to the translocation were detected at low levels for nearly one year after the cessation of releases (Lorimer 1981).

The second release experiment, using a translocation homozygote (T3) induced in *Ae. aegypti* from New Delhi, India, was conducted late in 1974 and early in 1975. During the initial nine weeks of releases 500 pupae, homozygous for both the translocation and the red-eye (re) mutation (Craig and Hickey 1967), were released daily in three villages (see Table 1). Owing to poor initial recovery, the genetic marker of the release stock was switched from *re* to *s* (spot) approximately mid-way through the experiment, and adult releases substituted for pupal. During the releases of translocation-homozygote adults, the frequency of the *s* phenotype rose from 1.8% to 45.0% among *Ae. aegypti* collected as eggs in the release villages and from 5.6% to 84.7% in adult landing collections (Lorimer, Lounibos and Petersen 1976). However, the frequency of *s* among pupae collected from clay pots was not significantly different from that in a reference village. Furthermore, there was no sign of decreased hatching capacity of eggs from females emerging from pots, which would have indicated wild-type X T3 homozygote matings in the field. Subsequent experiments revealed that the T3 homozygotes were deficient compared to wild Rabai *Ae. aegypti* in various measures of fitness, such as fertility, larval developmental time, larval and adult survivorship, and mating competitiveness. Most strikingly, oviposition substrate preferences of the T3 strain were markedly different from wild *Ae. aegypti aegypti* from Rabai, which preferred clay surfaces, while the translocated stock did not (Lorimer, Lounibos and Petersen 1976).

A final release was conducted in the main rainy season of 1975 using double translocation-heterozygote males produced by crossing T3 translocation homozygotes with another (T4) translocation homozygote isolated from *Ae. aegypti* from the Rabai area (Petersen, Lounibos and Lorimer 1977). Eggs from crosses of males of the T3/T4 heterozygote with wild-type females were 77% sterile. A mean of 517 translocation males was released daily for nine weeks into a village containing an estimated 1200 native *Ae. aegypti aegypti* adults (see Table 1). During releases, the hatching capacity of eggs from females captured at landing catches dropped from 93% to 30-40%. For more than eight weeks after the cessation of releases, egg hatching capacity levels gradually increased but remained lower than those in a nearby reference village. A decline in adult numbers in the release village occurred too early to be attributable solely to sterility induced by the translocation. Petersen, Lounibos and Lorimer (1977) concluded that insufficient sterility had been introduced to affect adult population size, which is regulated by density-dependent mortality of larvae in water jars.

Related ecological and genetic research on *Ae. aegypti* in the Rabai area

During the first heterozygote release in CHI, the domestic *Ae. aegypti* population in the nearest village, Kwa Dzivo (KDZ) was suppressed by sieving the contents of all water-storage jars twice weekly to remove and kill all mosquito larvae and pupae. This exercise eliminated a source of mosquito immigration, and the defaunated village served as a reference standard for *Ae. aegypti* population suppression (McDonald, Häusermann and Lorimer 1977). The absence of native mosquitoes in KDZ during the water-straining period did not, however, facilitate the colonization of this ‘empty niche’ by the T3 translocation homozygotes marked with red-eye (Lorimer, Lounibos and Petersen 1976).

Table 1. Experimental releases of translocated strains for the genetic control of *Ae. aegypti* in coastal Kenyan villages.

Release strain	Markers[1]	Objective	Villages[3]	Population size[2]	Release period	Nos./day	Results	Reference
Mixed single and double translocation heterozygotes	Spot (*s*) Silver (*Si*)	Suppression by induced sterility	CHI	635	March –June 1974	814	Sterility >60% but no population suppression	McDonald et al. (1977)
Translocation homozygote (T3)	Reference (*re*), *s*[4]	Population replacement	MGN KBW KDZ	955 ± 488 797 ± 270 --------[5]	Oct – Dec 1974; Jan –March 1975	500	No detection of re-T3, s-T3 recovered but not in water pots	Lorimer et al. (1976)
Double translocation heterozygote (T3/T4)	s Black tarsi (*blt*)	Suppression by induced sterility	MBI	1,200 ± 285	Apr - June 1975	813	Sterility 60-70% but no population suppression	Petersen et al. (1977)

[1] Morphological genetic markers described in Craig and Hickey (1967)
[2] Estimates with mean ± SE are by the method of Jolly (1965) applied to mark-recapture data; Bailey's triple-catch method used in CHI
[3] CHI = Chibarani; MGN = Mgandini; KBW = Kwa Bendegwa; KDZ = Kwa Dzivo; MBI = Mn'gamboni
[4] Red-eye marked mosquitoes were released for the first 12 weeks, nine weeks as pupae, three weeks as adults; subsequent T3 releases, marked with Spot, had wild-type eye colour
[5] Native *Ae. aegypti* in KDZ had been suppressed by water sieving prior to *re*-T3 release; only MGN and KBW were used for *s*-T3 release

The suppression by water sieving performed in KDZ was repeated in Mwamrundogo (MWN) for 16 consecutive weeks from late 1974 through early 1975 to corroborate the results in KDZ, to examine the time course of recolonization by *Ae. aegypti* after the conclusion of pot cleaning, and to investigate house entry by *Ae. aegypti formosus* in the absence of its domestic conspecifics. Egg numbers from ovitraps and adults from landing catches began to decline in MWN in comparison to a reference village less than two weeks after the onset of water sieving (see Figure 1). With one exception, egg and adult numbers remained below reference-village levels for at least five weeks after the conclusion of pot cleaning. No evidence for increases in house entry by *Ae. aegypti formosus* was detected during the suppression period (Petersen 1977).

Container-inhabiting mosquitoes of the Rabai area were censused for approximately 18 months by suspending water-holding bamboo sections to monitor oviposition in different vegetation zones. Among 22 mosquito species recovered, *Ae. aegypti formosus* was most abundant in cultivated and ecotonal zones of a vegetation transect (Lounibos 1981). Among six other related species of the subgenus *Stegomyia* common on this transect, *Aedes metallicus* was most abundant close to houses, and the two forest species, *Aedes heischi* and *Aedes soleatus,* were spatially segregated by preferences for different heights from the forest floor (Lounibos 1981).

Petersen (1977) performed a series of releases of native *Ae. aegypti formosus* and *Ae. aegypti aegypti* to investigate their behaviour and habitat fidelity, as well as to seek evidence for their hybridization, in village environments. When virgin female *Ae. aegypti formosus* were released simultaneously with male *Ae. aegypti aegypti*, significantly more offspring of intermediate phenotype were collected in the release village compared to a reference village. Releases of both sexes of *Ae. aegypti formosus* resulted in some increases of this form in indoor ovitraps. Overall, Petersen's (1977) release experiments supported the accumulating evidence that these subspecies are usually segregated by distinctive habitat preferences and biting behaviour (McClelland 1960; McClelland and Weitz 1963), but population growth and dispersal of the feral subspecies during the rainy season increases the potential for hybridization between the forms and occasional house entry by *Ae. aegypti formosus.*

Isozyme electrophoresis was performed on *Ae. aegypti aegypti* samples collected from two villages (MGN and MAJ) over the course of one year. Analyses of 23 enzyme loci indicated temporal stability of gene frequencies but significant differences between villages (Tabachnick and Powell 1978). These results suggested that individual villages were panmictic units, a condition which has important implications for vector control by genetic modifications. Isozyme methods also elucidated the genetic relationships among populations of feral *Ae. aegypti formosus* from Rabai and elsewhere on the Kenya coast and to indoor *Ae. aegypti aegypti* from three villages (MAJ, MGN, KBW). Genetic distances obtained from allele-frequency data confirmed the genetic distinctness of the sympatric feral and domestic forms but were not sufficiently high to preclude restricted gene flow between these morphs and did not warrant their description as separate species (Tabachnick, Munstermann and Powell 1979).

Subra (1983) examined the population dynamics of *Ae. aegypti aegypti* pupae in KBW village by daily counts of pupae in all 53 indoor water pots, coupled with observations on domestic water use in that community. He determined that the rhythm of water replenishment and the accidental introduction of food into water jars regulated pupal numbers. If water replenishment occurred more often than once per week, pupal numbers were low. Among pots with less frequent water renewal, pupal

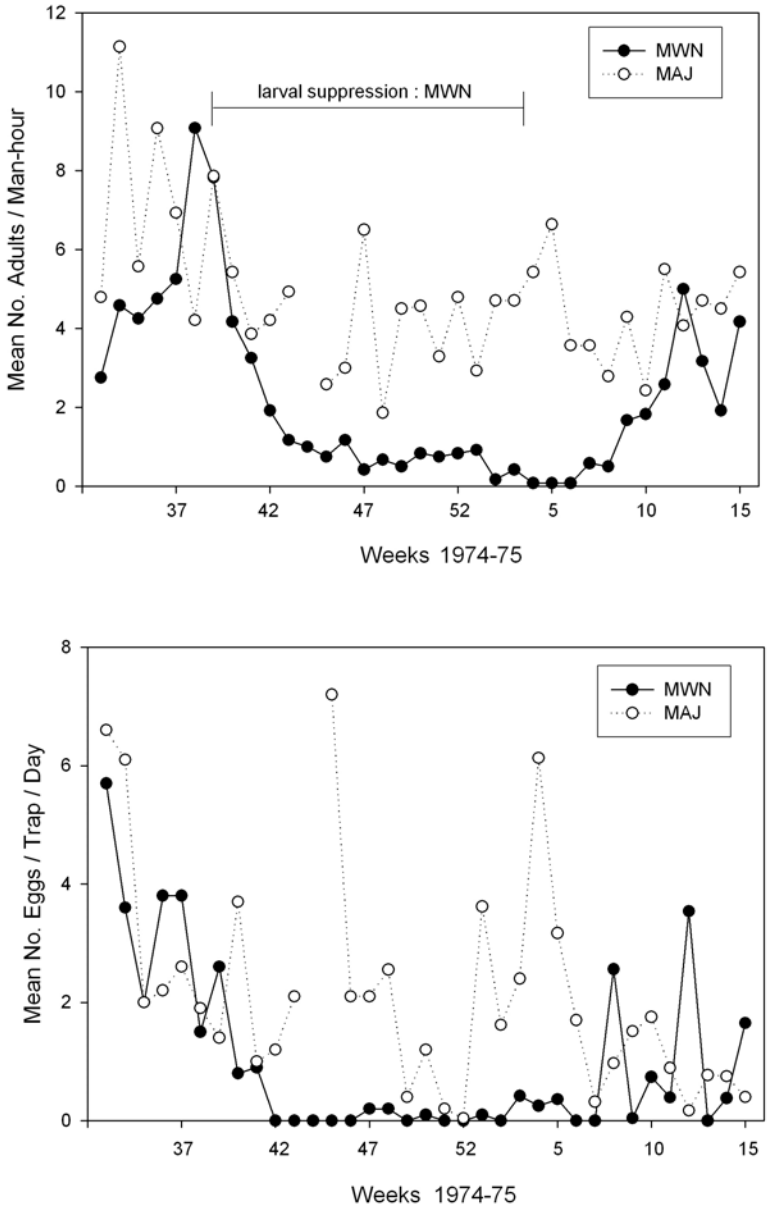

Figure 1. Mean numbers of eggs and adult *Ae. aegypti* captured per day in a reference village (MAJ) and in a neighbouring village (MWN) in which all domestic water pots were sieved twice weekly, for 16 weeks as indicated in the top-panel inset, to remove the aquatic stages of this species. Eggs were collected on cloth oviposition strips set for three days per week in each house of MAJ (n=28) and MWN (n=24). Weekly landing collections of adults were performed by three collectors who spent 10 minutes in each house during the mid-morning biting interval of *Ae. aegypti.*

productivity was especially high in houses where young children introduced maize gruel into pots when withdrawing water with a ladle that had been contaminated with food particles by prior contact with the mouths or hands of the children.

Subsequent experimental manipulations of the contents of water jars in KBW showed that addition of maize gruel, but not of first instar *Ae. aegypti* larvae, significantly increased pupal productivity (Subra and Mouchet 1984). These results confirmed the natural surfeit of *Ae. aegypti* eggs in breeding containers and the density- and resource-dependent nature of population regulation in this species. Subra and Mouchet (1984) cautioned that population suppression of *Ae. aegypti* by introduced sterility would succeed only if egg hatching capacity could be reduced to a very low (still unknown) level.

Conclusions and postscript

The releases of translocated *Ae. aegypti* into Rabai villages were driven by the schedule of a generous but time-limited contract from USAID. Biological characteristics of the translocation strains, especially their fitness relative to native *Ae. aegypti*, were poorly known prior to releases because the exigency to fulfil the principal objective of the project, i.e. to perform releases, outweighed a more systematic approach that incorporated thorough pre-testing. Translocations suitable for release were neither as easy to isolate or to propagate as had been hoped, which limited the sources of mosquitoes available for release while the funding-agency clock was ticking. For example, the release in Kenya of genetically modified *Ae. aegypti* of Indian origin was *a priori* inappropriate, but no other translocation homozygote was available to perform this proposed experiment. Also, although the release environment for adult *Ae. aegypti* in the Rabai area was reasonably well characterized, little thought and no research was committed to investigating the underlying factors controlling population regulation, such as density-dependent larval development, which elsewhere had been previously identified in *Ae. aegypti* (Southwood et al. 1972) and might resist genetic control.

Despite such shortcomings, the MBU project can be regarded as successful in terms of new insights into the ecology, behaviour and genetics of natural *Ae. aegypti* populations. Highlighted discoveries include the genetic distinctness of sympatric *Ae. aegypti formosus* and *Ae. aegypti aegypti*, and the impact of larval density dependence and human behaviour in regulating domestic *Ae. aegypti* populations. Unfortunately, because the genetic-control experiments did not succeed in suppressing *Ae. aegypti*, some of the more basic and enduring contributions of MBU have been obscured by the failures of the project's more feted and applied objectives. In addition to the research accomplishments on *Ae. aegypti*, related projects at MBU and the ICIPE Coastal Research Station produced important insights into the ecology of other container-inhabiting mosquito species and of coastal vectors of human filariasis and malaria.

In the context of renewed interest of manipulating the genetics of natural mosquito populations (e.g. Scott et al. 2002; Alphey et al. 2002), at least four lessons from the MBU experience may be instructive: (1) the population dynamics of the target population needs to be well understood before introducing the foreign element(s); (2) the fitness of the released mosquitoes relative to wild targets requires rigorous testing; (3) if population suppression via introduced sterility (e.g. Curtis 2002) is an objective, sterility levels must be very high to reduce adult numbers of species such as *Ae.*

aegypti; (4) changes in human behaviour might accomplish reductions in vector-human contact more simply than genetic-control interventions.

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