

POTENTIAL FOR DENGUE IN SOUTH AFRICA: MOSQUITO ECOLOGY WITH PARTICULAR REFERENCE TO *Aedes aegypti*

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ABSTRACT. Observations on prevalence, geographical distribution, utilization of artificial larval habitats and anthropophilism were made on diurnal mosquitoes at selected localities along the coast of Natal and inland in the Transvaal to identify potential vectors of dengue in South Africa. Larval collections made in artificial containers on the ground, the exposure of bamboo pots as ovitraps in trees and collection of mosquitoes biting man showed the following species as the most likely candidates for vectors: *Aedes aegypti*, *Ae. demeilloni*, *Ae. simpsoni*, *Ae. strelitziae*, *Ae. furcifer*, *Ae. cordellieri* and *Eretmapodites quinquevittatus*. The bamboo pots showed that *Ae. aegypti* and *Ae. simpsoni* were the most widespread species, occurring at 11 of 12 localities. *Aedes aegypti* was the most prevalent species with mean pot index of $60.3 \pm 9.8\%$ (SE) and abundance index of 0.43 ± 0.15 (SE). *Aedes aegypti* was frequently present as larvae in artificial containers at indices of 11–83% (mean $56.8 \pm 5.6\%$, SE) and was the most anthropophilic species with average biting rates of 10–29 per man-hour at 7 localities. Although *Ae. aegypti* was abundant in the pots at Ndumu (northern Natal) and at Skukuza (eastern Transvaal), the local populations were poorly anthropophilic at these localities. At some localities, populations of *Ae. demeilloni*, *Ae. simpsoni* and *Ae. strelitziae* had average biting rates of 5.4–9.6 per man-hour. *Aedes furcifer* was collected for the first time at Durban, extending its distribution southward to latitude $29^{\circ}53'S$.

INTRODUCTION

Investigations of dengue vectors in countries outside South Africa have only incriminated aedine mosquitoes, mostly of the subgenus *Stegomyia*. The rural endemic vector in Asia is *Aedes (Stg.) albopictus* (Skuse), while the urban vector in Asia, West Africa and tropical America is *Ae. (Stg.) aegypti* (Linn.) (Gubler 1988). In West Africa, other *Stegomyia* species apparently play the role of enzootic sylvan vector, together with 2 species of the subgenus *Diceromyia*, i.e., *Ae. furcifer* (Edwards) and *Ae. taylori* Edwards (Cordellier et al. 1983, Roche et al. 1983). *Aedes aegypti* is widespread in the tropical and subtropical areas in eastern South Africa (Muspratt 1956), while *Ae. furcifer* is limited to the tropical areas of northern Natal and the northeastern Transvaal (Jupp 1980).

Our Arbovirus Unit is engaged in a project designed to investigate tree hole and container breeding *Aedes* species, principally members of the subgenera *Stegomyia* and *Diceromyia*, in eastern South Africa. The objective is to assess these mosquitoes as potential vectors of dengue viruses which could participate in epidemic transmission should dengue be reintroduced into the country. The project has several aspects which have already been defined in a publication on the taxonomic status of *Ae. aegypti* populations (Jupp et al., in ms.). This study is concerned with the ecology of potential vectors. Collecting localities were chosen along the Natal coast and at Skukuza in the eastern Transvaal as representing points where a dengue outbreak

might begin. Furthermore, Ndumu (Natal) and the Magaliesberg and Mica (Transvaal) were chosen primarily for investigations of non-anthropophilic populations of *Ae. aegypti*, while Tzaneen (northern Transvaal) was selected for its anthropophilic population; these *Ae. aegypti* collections were relevant to the taxonomic study (Jupp et al., in ms.). Observations were made on prevalence, geographical distribution, utilization of artificial containers as larval habitats and diurnal biting activity on human bait to determine to what extent different species possessed ecological attributes which made them likely dengue vectors.

MATERIALS AND METHODS

Ovitraps in trees: Bamboo pots simulating tree holes were exposed as ovitraps to collect tree hole breeding mosquitoes. Eggs, larvae and pupae were obtained from the various localities mapped in Fig. 1 by exposing bamboo pots for extended periods ranging from 38 to 153 days between November 7, 1989, and May 17, 1990. Eggs were also obtained by exposing black plastic bottles of water containing wooden paddles for oviposition (Jupp and McIntosh 1990) on a farm in the Magaliesberg mountains and at Mica. The ovitraps were suspended in shady trees at heights ranging from 1 to 4 m above ground level. At the end of the exposure period, ovitraps were returned to the laboratory where the eggs were hatched by flooding with tap water and adults reared out. The bamboo pot index for each species is defined as the percentage of

pots found to contain that species. The abundance index is the number of mosquitoes at each locality divided by the product of the number of pots and number of days they were exposed.

Artificial containers: Mosquito larvae were sampled from water-retaining artificial containers in motor car scrap yards, municipal rubbish dumps and other peridomestic sites at various localities in Natal and in the Transvaal (Fig. 1) from November 5, 1988, to April 18, 1989. The following containers had culicine larvae and pupae: used tire casings (most commonly), metal drums, floor pans and tire wells in scrapped cars, paint cans, beverage cans and beverage cartons. Samples were taken from tires containing water and leaf litter by dipping a ladle repeatedly into the water until at least 50 larvae and/or pupae had been obtained, or at least 3 times until it was evident that no culicines were present. The other, more accessible containers were scrutinized for immature culicines. Larvae were reared out in the laboratory and identified. Container indices were recorded as the percentage of containers found to contain *Ae. aegypti*.

Human-baited collections: These collections were carried out during the daytime because *Ae. aegypti* and other species of *Stegomyia* are diurnal biters. Volunteers used test tubes to collect adult female mosquitoes which probed and engorged on their bare legs and feet. The biting rates thus obtained were based on 2-5 volunteers collecting in the open at suitable sites, usually near artificial containers in the urban localities and the bamboo pot sites at Palm Beach, Armadale, Ndumu and Tzaneen. Collections were made over the months of January to April 1989, November 1989 to February 1990 and January to February 1991, usually during 2 periods of the day, 0530-0930 h and 1500-1900 h. No collections were undertaken during the crepuscular periods or at night. Collecting generally took place on days when the prevailing climatic conditions were warm, humid, partly cloudy and calm; mosquitoes remained active during slightly windy conditions. Mosquitoes were separated according to species, and biting rates were calculated by combining data from several collections per locality and dividing by the total number of man-hours invested (the collection effort). Observations were made on various aspects of feeding behavior.

Mosquito identification: The mosquito nomenclature follows that of Knight and Stone (1977) and Ward (1984) except where more recent taxonomic revisions have occurred. These relate to the transfer of certain *Ae. (Aedimorphus)* species into the subgenus *Albuginosus* of *Aedes* (Reinert 1986) and the description of *Ae. (Diceromyia)*

cordellieri Huang in the *Ae. furcifer* group (Huang 1986a).

RESULTS

Ovitrap in trees: The results of the survey for tree hole breeding mosquitoes by means of bamboo pots are given in Table 1. Twenty-eight species in 3 genera were sampled at 8 localities in Natal and 4 localities in the Transvaal (Fig. 1). *Toxorhynchites brevipalpus* Theobald and *Ae. aegypti* utilized the pots most frequently at the Natal localities (mean bamboo pot indices > 50%). The most abundant species in Natal were, in order, *Ae. dendrophilus* Edwards, *Ae. capensis* Edwards and *Ae. aegypti*, while the most widespread were, in order, *Tx. brevipalpus* and *Ae. simpsoni* (Theobald) followed by *Ae. aegypti*, *Ae. dendrophilus* and *Ae. capensis*. At the Transvaal localities *Ae. aegypti* had the highest pot index and was the most abundant and widespread species.

Overall, *Ae. aegypti* and *Ae. simpsoni* occurred at 11 of the 12 South African localities. *Aedes aegypti* was found most often in the bamboo pots (mean pot index = $60.3 \pm 9.8\%$, SE) and was the most abundant species (mean abundance index = 0.43 ± 0.15 , SE) except for *Ae. dendrophilus* (mean abundance index = 0.47 ± 0.26).

In the subgenus *Diceromyia*, *Ae. cordellieri* occurred in bamboo pots at Ndumu in northern Natal and, to a small extent, at Skukuza in the eastern Transvaal. *Aedes furcifer* utilized the bamboo pots in Durban, Ndumu and Skukuza with pot indices of 20, 71 and 47%, respectively. The abundances of the 2 species were low in all cases.

Artificial containers: Container indices were determined for *Ae. aegypti* (Table 2) because this was by far the most prevalent species occurring as larvae in artificial containers on the ground and because of the known importance of the species as a vector of dengue and other viruses outside South Africa. Nine of the 14 localities where containers were sampled had container indices greater than 50%, with the 3 highest occurring at Port Shepstone (83%), Empangeni (78%) and Durban (76%). Other species quite frequently encountered in these containers were *Ae. simpsoni*, *Eretmapodites quinquevittatus* Theobald, *Tx. brevipalpus* and *Culex quinquefasciatus* Say. The first 3 of these species were also found to be common in containers sampled in Eshowe in Natal, although *Ae. aegypti* was uncommon when that locality was sampled in November 1988.

Water-retaining plants: Larvae and pupae of *Ae. simpsoni* and *Ae. strelitziae* Muspratt were

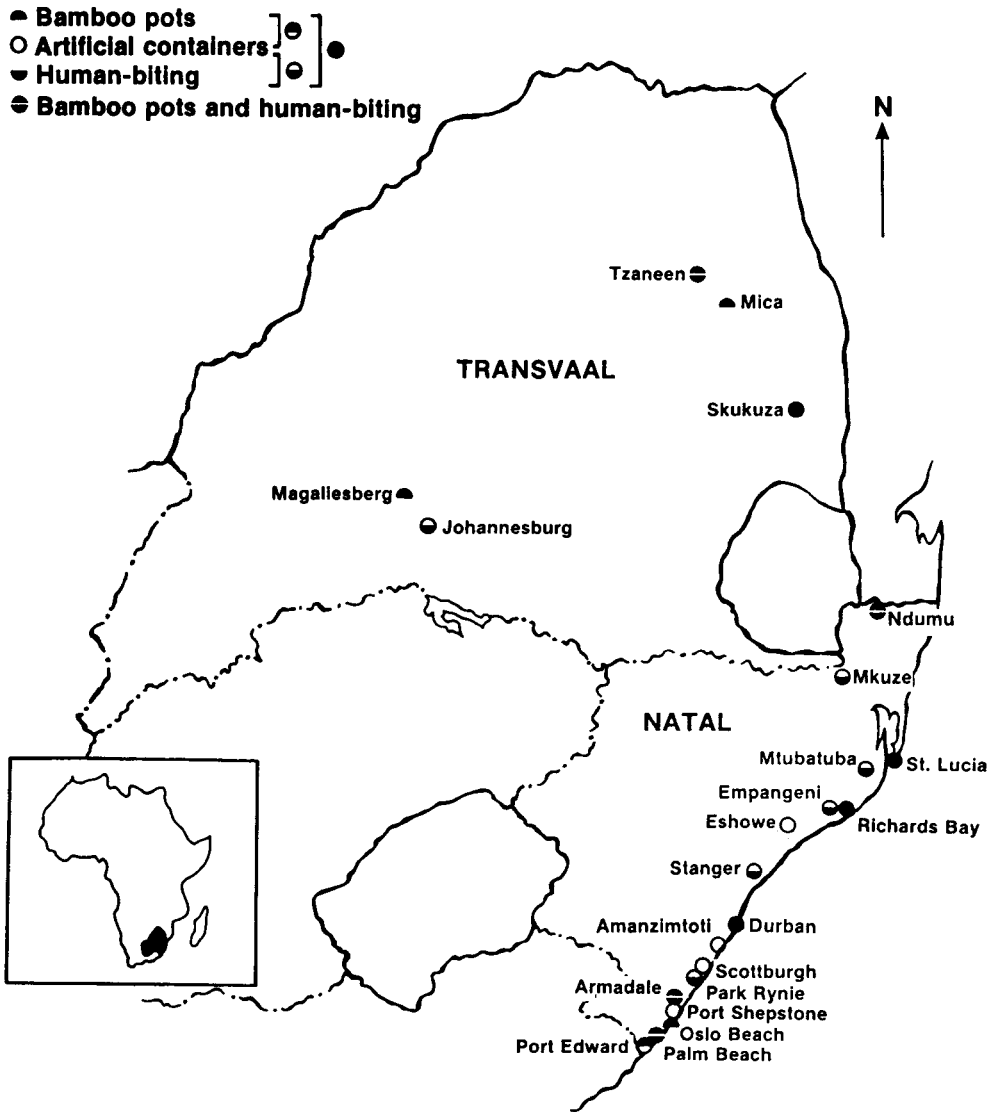


Fig. 1. South African localities where mosquitoes were sampled in bamboo pot ovitraps in trees, in artificial containers on the ground and by diurnal human baited collections.

collected from the leaf axils of *Strelitzia nicolai* Regel and Koern (Strelitziaceae) at Palm Beach and the immatures of *Ae. demeilloni* Edwards, *Ae. simpsoni* and *Er. subsimplicipes* Edwards from *Dracaena hookeriana* Koch (Agavaceae) at Oslo Beach. Large stands of *Strelitzia nicolai* and *Dracaena hookeriana* were also found in undisturbed, indigenous, coastal forest on the farm, Armadale, about 14 km north of Port Shepstone. *Eretmapodites quinquevittatus* larvae were collected from the dried, opened husks of the fruit of the black or spineless monkey

orange tree, *Strychnos madagascariensis* Poirlet (Loganiaceae), at St. Lucia Estuary.

Human-baited collections: Biting rates, as a measure of anthropophily, were significant for *Ae. aegypti* at 7 of the urban localities (10–29 per man-hour: Table 2), although the Johannesburg sample is probably not from a perennial population. Biting rates were generally low at localities in Natal further north than Empangeni, correlating with generally low abundances (Table 1). Two adult collections at a Durban site, spaced one month apart in early 1991, gave

Table 1. Survey with bamboo pots for mosquitoes at various localities; bamboo pot indices (% of positive pots); and, in parentheses, abundance indices (no. mosquitoes/no. pots/no. days exposed).

	P. Edw.	Palm B.	Oslo B.	Armada	Durban	R. Bay	St. Lucia	Ndumu	Magal.	Skukuza	Mica	Tzaneen
No. of pots	5	10	15	6	15	14	23	44	22	23	26	15
No. of days exposed	57	57	57	57	57	57	56	64	112	153	31	38
<i>Ae. (Alb.) capensis</i>	100 (1.16)	80 (1.68)	0	67 (1.07)	0	0	57 (0.25)	30 (0.09)	0	0	0	0
<i>haworthi</i>	0	0	0	0	0	0	0	0	0	9 (0.01)	0	0
<i>kennethi</i>	0	0	0	0	0	0	0	34 (0.05)	0	0	0	0
<i>marshali</i>	0	0	0	0	0	0	0	0	36 (0.01)	57 (0.016)	0	40 (0.08)
<i>Ae. (Dic.) adersi</i>	0	0	0	0	7 (<0.01)	64 (0.17)	0	0	0	0	0	0
<i>cordelieri</i>	0	0	0	0	0	0	0	29 (0.02)	0	5 (<0.01)	0	0
<i>furcifer</i>	0	0	0	0	0	0	0	71 (0.04)	0	47 (0.02)	0	0
<i>furcifer</i> group	0	0	0	0	20 (0.02)	0	0	32 (0.05)	0	39 (0.01)	0	0
<i>Ae. (Fin.) fulgens</i>	0	0	0	0	0	0	0	7 (0.02)	0	17 (<0.01)	6	13 (0.03)
<i>Ae. (Psa.) natalensis</i>	0	0	7 (0.05)	0	0	0	35 (0.06)	0	0	0	0	0
<i>Ae. (Stg.) aegypti</i>	40 (0.10)	100 (1.17)	93 (0.85)	0	53 (0.14)	50 (0.07)	9 (<0.01)	73 (0.35)	45 (0.01)	100 (0.65)	67	93 (1.39)
<i>continguus</i>	0	0	0	0	0	0	0	0	50 (0.05)	0	0	0
<i>demeilloni</i>	20 (0.02)	30 (0.02)	7 (<0.01)	33 (0.04)	0	0	0	0	0	0	0	0
<i>dendrophilus</i>	100 (1.53)	100 (1.30)	20 (0.05)	100 (2.74)	0	0	4 (<0.01)	16 (0.02)	0	7 (<0.01)	0	0
<i>heischi</i>	0	0	0	0	0	0	0	48 (0.10)	0	0	0	7 (0.01)
<i>ledgeri</i>	0	0	0	0	0	0	0	11 (0.01)	0	87 (0.36)	44	47 (0.73)
<i>metallicus</i>	0	0	0	0	0	0	0	41 (0.08)	0	100 (0.28)	39	47 (0.14)
<i>simpsoni</i>	20 (0.02)	70 (0.46)	33 (0.15)	17 (0.01)	13 (0.01)	7 (0.02)	4 (<0.01)	68 (0.14)	5 (0.03)	70 (0.15)	0	33 (0.08)
<i>soleatus</i>	0	0	0	0	0	0	87 (0.74)	11 (0.01)	0	0	0	0
<i>strelitziae</i>	0	30 (0.03)	13 (0.01)	0	0	0	0	0	0	0	0	0
<i>unilineatus</i>	0	0	0	0	0	0	0	5 (<0.01)	0	13 (<0.01)	6	0
<i>Cx. (Cux.) pipiens</i>	0	0	0	0	0	0	0	0	14	0	0	0
<i>zombaensis</i>	0	0	0	0	0	0	0	2 (<0.01)	5	0	0	0
<i>Cx. (Cui.) cinerellus</i>	0	0	0	0	0	0	0	20 (0.01)	0	0	0	0
<i>cinereus</i>	0	0	0	0	0	0	0	23 (0.05)	0	0	0	0
<i>nebulosus</i>	0	0	13 (0.02)	0	7 (0.03)	0	9 (0.03)	20 (0.04)	0	4 (<0.01)	0	7
<i>Cx. (Eum.) horridus</i>	0	0	0	0	0	0	0	16 (0.01)	0	48 (0.21)	0	7
<i>Cx. (Lut.) tigripes</i>	0	0	0	0	0	0	0	0	5	0	0	0
<i>Tx. (Tox.) brevipalpus</i>	100	88	27	60	40	43	61	66	0	0	0	0

Table 2. *Aedes aegypti* collections at various localities: artificial container indices for larvae and average biting rates in human-baited collections.

Locality*	Larval collections		Adult collections	
	No. containers examined	Container index (%)	Man-hours	Biting rate (per man-hour)
<i>Natal</i>				
Port Edward	17	47	—	—
Oslo Beach	—	—	2.0	0
Palm Beach	NF**	—	31.2	11.2
Port Shepstone	18	83	—	—
Park Rynie	37	54	4.0	18.0
Scottburgh	19	11	—	—
Durban	45	76	9.0	29.0
Stanger	13	54	5.0	12.4
Empangeni	18	78	4.5	18.0
Richards Bay	53	62	23.5	1.5
Mtubatuba	21	33	5.5	2.9
St. Lucia	9	56	8.0	0.8
Mkuze	10	70	5.5	3.5
Ndumu	NF	—	5.0	0.2
<i>Transvaal</i>				
Johannesburg	33	45	2.0	13.0
Skukuza	10	70	1.8	0.5
Tzaneen	—	—	1.0	10.0

* All localities are urban except for Ndumu, which is rural; all sites in the urban localities are peridomestic except at Johannesburg, where it is domestic.

** NF = no artificial containers found.

biting rates of 15 and 89 per man-hour, respectively. Both collections had taken place during the midday period, defined for our purposes as 1000–1500 h. Rainfall totals over 30 days prior to each collection were 43 mm for the first and 263 mm for the second. The Ndumu and Skukuza populations, known and assumed to be non-anthropophilic, respectively, had biting rates lower than 1 per man-hour even though they were prevalent in the bamboo pots (Table 1).

Male mosquitoes subsequently captured and identified as *Ae. aegypti* were often observed to swarm in small numbers (rarely greater than 10) about the bait, a man's exposed leg and foot. Within minutes of swarm-formation, the conspecific females arrived at the bait. They were immediately approached by the males and copulation ensued in the air. Mating mosquitoes either remained *in copula* in flight or landed on the ground or on the bait to mate. The females then approached the bait to feed. Female *Ae. aegypti* were often slow to alight before feeding, particularly if a slight breeze was blowing. Males also alighted on the bait but apparently only to rest, because as soon as females approached, the males would fly up to meet them. Occasionally, females arrived and fed on the bait without the presence of males in the vicinity. Similar behavior patterns were observed for *Ae. demeilloni*

and *Ae. strelitziae*, whereas males of *Ae. simpsoni* and *Er. quinquevittatus* commonly occurred at and rested on the bait. At Palm Beach, where no obvious concentration of larval habitats other than water-retaining plants occurred, the diurnal, anthropophilic mosquitoes were only collected in small numbers at any one site. It was necessary to move regularly over small distances to find fairly large numbers of these species biting.

Four *Stegomyia* species other than *Ae. aegypti* were taken in the human-baited collections. Their average biting rates are shown in Table 3 together with the rate for *Er. quinquevittatus*. *Aedes demeilloni* was found to bite readily during the midday period. The biting rates measured in 1991 were 13 per man-hour at Armadale (collection effort = 4.2 man-hours between 1000 and 1215 h) and 38.8 per man-hour at Palm Beach (collection effort = 1.7 man-hours between 1155 and 1250 h). *Aedes simpsoni* was only encountered at high biting rates in Johannesburg in the late afternoon. *Aedes strelitziae* was the most common anthropophilic species at Armadale, with biting rates ranging from 8.7 to 16.3 per man-hour, the higher obtained during 1000–1215 h (collection effort = 4.2 man-hours). *Eretmapodites quinquevittatus* was not commonly collected as adults except for a site in Richards Bay where the biting rate in December 1989 was

Table 3. Daytime human-baited collections at various localities; average biting rates of the most prevalent species other than *Aedes aegypti*.

Species	Biting rate (per man-hour)	Locality
<i>Ae. (Stg.) demeilloni</i>	5.4	Palm Beach
	5.5	Armadale*
<i>dendrophilus simpsoni</i>	0.1	St. Lucia Estuary
	1.2	Palm Beach
	2.0	Oslo Beach
	0.5	Park Rynie
	0.2	Richards Bay
	0.3	St. Lucia Estuary
	7.5	Johannesburg
	0.5	Skukuza
	2.5	Palm Beach
	9.6	Armadale*
0.4	Richards Bay**	
<i>Er. quinquevittatus</i>	0.7	Palm Beach
	0.6	Stanger
	2.3	Richards Bay
	0.2	Mtubatuba
	0.9	St. Lucia Estuary

* Collection effort = 15 man-hours.

** Collection effort = 14 man-hours.

10 per man-hour (collection effort = 2 man-hours in the late afternoon).

No evidence of the exotic species, *Ae. albopictus*, was found in the course of this survey, despite the recent discovery of immatures in tire casings imported from Southeast Asia and landed in Cape Town (Hunt et al. 1990).

DISCUSSION

Our study has concentrated on particular areas of South Africa. First, those where dengue is likely to be successfully introduced into the country via the shipping and tourist industries and, second, where the most probable vectors, the *Stegomyia* and *Diceromyia* species, are to be found. The characteristics of potential vectors are their appropriate distribution, abundance and anthropophilic behavior. If a species is a known vector of dengue virus outside South Africa, this is also an important consideration. *Aedes aegypti* and *Ae. furcifer* are dengue vectors elsewhere (Gubler 1988, Roche et al. 1983). *Aedes cordellieri* must also be considered, even though its potential for dengue transmission is unknown. A dengue 2 epizootic in the Ivory Coast and Upper Volta was associated with *Ae. furcifer* and *Ae. taylori* (Cordellier et al. 1983). More recently Huang (1986a) has described *Ae. cordellieri*, a third member of the *Ae. furcifer* group from the same region, and it is possible that this species may have played a role in the epizootic. *Aedes demeilloni*, *Ae. simpsoni*, *Ae.*

strelitziae and *Er. quinquevittatus* are potential vectors of dengue because of their domestic or peridomestic occurrence. Each species will be discussed in the above order.

Aedes aegypti: The adult mosquito can survive under widely variable climatic conditions, and anthropophilic populations occur in the southeastern Cape Province at Grahamstown (Edwards 1941; Jupp, unpublished data) and East London (Mattingly 1953; Kemp, unpublished data), both above 33°S latitude. Furthermore, the species is represented by established populations at a variety of altitudes ranging from near sea level to 1,800 m (Johannesburg) in South Africa, mainly associated with wooded savannah (bushveld) and forest (coastal scrub, riverine and montane) or with the urban environment (Muspratt 1956). This species has become adapted to a wide range of larval habitats ranging from natural tree holes and leaf axils to artificial containers in the domestic and peridomestic environments (Hopkins 1952, Horsfall 1955).

The southern Natal coast has been urbanized extensively to cater for the tourist industry, and the endemic populations of *Ae. aegypti* appear to have adapted to utilize the peridomestic environment. These local populations were shown to be highly anthropophilic (Table 2) and could constitute a serious health hazard should they be found to be efficient vectors of dengue. In northern Natal the urban areas are fewer and less developed except for Richards Bay, an international harbor. High densities of anthropophilic *Ae. aegypti* were not as evident in our collections at these localities, although container indices (Table 2) were significant at the collection sites which consisted mainly of tire dumps. The collections at Ndumu, a relatively undeveloped game reserve on the Mozambique border, are considered to represent a non-anthropophilic population of *Ae. aegypti*. Artificial containers were not present at this locality. An extensive series of human-baited collections in the reserve (McIntosh et al. 1972) failed to demonstrate *Ae. aegypti* in gallery forest dominated by *Ficus sycamorus* Linn. (Moraceae). This was confirmed by the present adult collections at the same site, even though ovitraps yielded abundant eggs of *Ae. aegypti* (Table 1).

The Transvaal collections include anthropophilic populations of *Ae. aegypti* from Johannesburg in the south and Tzaneen in the north. The Johannesburg population, however, is probably not an established one, i.e., does not overwinter there. At least some of the tires which formed the larval habitats were imported via Durban, and it is probable that *Ae. aegypti* eggs were introduced with the tires. The relevant site was

on the grounds of a small business concern which reprocessed the rubber from tires into commercial goods, e.g., sandals. This illustrates the unusual mode of range extension in the form of eggs being dispersed by the used tire industry, not only intercontinentally as in the case of *Ae. albopictus*, but from the subtropical region where the species is endemic to the temperate region which can support the species during the summer in South Africa.

Egg collections were made at a farm in the Magaliesberg mountains, Skukuza in the Kruger National Park and a game farm near Mica to sample what were considered to be non-anthropophilic populations due to their feral nature. Limited human-baited collections at the Magaliesberg locality proved negative for *Ae. aegypti* and more extensive collections at Skukuza yielded few adults, in spite of the presence of the species in ovitraps at both localities. Skukuza, paradoxically, is an urban locality in a game reserve and consists of a large staff village associated with an industrial site (workshops and light industry) and tourist camp. The Mica locality in the wooded savanna region of the northeastern Transvaal yielded collections of *Ae. aegypti* in ovitraps. Human-baited collections were not attempted, as an earlier study (Jupp and McIntosh 1990) described the non-anthropophilic nature of the population.

The strong diurnal pattern in the biting activity of *Ae. aegypti* is well known. However, the possibility of biting peaks just after sunrise and just before sunset was indicated by the work of Reed and colleagues in 1901 (see Horsfall 1955) and that of Trpis et al. (1973). This was the basis for the timing of our human-baited collections. There is also strong evidence that major biting peaks exist in the hour before midday (Teesdale 1959) and from 1200 to 1400 h and during the crepuscular periods (Lumsden 1957). Biting activity during the daytime hours outside of our standard periods was demonstrated in the present study: the Durban and Palm Beach populations of *Ae. aegypti* were collected from 1000 to 1500 h at very high biting rates.

Twenty-four-hour human-baited collections yielded biting rates for *Ae. aegypti* of up to 13.4 per man-hour during the 1952-53 epidemic of chikungunya fever in Tanzania (Lumsden 1955). Trpis et al. (1973) made extensive recordings of landing rates on man for the species in an automobile dump in Dar-es-Salaam, Tanzania. The landing rate is an approximation of biting rate, and if one extracts their data for periods in the day corresponding to the times when our collections were made, a rate of 9.9 per man-hour is obtained. The biting rates for the anthropophilic populations of *Ae. aegypti* in

South Africa are thus comparable to those reported from East Africa. The occurrence of a highly anthropophilic, peridomestic population in the metropolis of Durban is potentially very important in terms of epidemiology.

Aedes furcifer: Our study was not designed to sample adults of this species, which is primarily nocturnal with a crepuscular activity peak just after sunset (Port and Wilkes 1979). The *Ae. furcifer* group was previously thought to be confined to the tropical regions with the southernmost distribution being in the region of Lake St. Lucia (28°S latitude) on the 18°C midwinter isotherm (Jupp and McIntosh 1988). *Aedes furcifer sensu strictu* was found in the ovitraps placed in a horticultural nursery in the suburb of Congella in Durban at 29°53'S latitude (Table 1). However, the abundance of the mosquito in the bamboo pots was low and the epidemiological threat may consequently be slight. Sizable populations only occur after heavy summer rainfall in the often drier wooded savanna of northern Natal and the northeastern Transvaal (Jupp and McIntosh 1988). Because it has been established as a vector of dengue in West Africa (Cordellier et al. 1983), it must be regarded as a potential vector in the tropical regions of South Africa.

Aedes cordellieri: As for the previous species, experimental design precluded the collection of adults of the nocturnally active *Ae. cordellieri*. It was present during the rural epidemic at Mica (McIntosh et al. 1977), being identified then as *Ae. taylori*. It constituted about 1% of the *Ae. furcifer/cordellieri* total based on the proportion of males collected (Jupp and McIntosh 1990). This species was represented in the ovitraps in the tropical region in association with *Ae. furcifer* (Table 1). The abundance in the bamboo pots appeared to be too low for the species to be considered epidemiologically important, even though it must be considered a potential vector of dengue due to its taxonomic and behavioral similarity to *Ae. furcifer*.

Aedes demeilloni: This species is limited to the eastern coastal plain largely due to special habitat requirements. The leaf axils and apical crown of the plant, *Dracaena hookeriana*, form the natural breeding places (Muspratt 1956). Even though *Ae. demeilloni* was found in bamboo pots and sometimes in artificial containers on the south coast of Natal, these populations appear to be dependent on the presence of large stands of *Dracaena* spp. *Aedes demeilloni* is a highly anthropophilic species, as the 1991 collection at Palm Beach shows. Muspratt (1956) reports biting rates of 30-50 per man-hour further south at Port St. Johns on the Transkei coast. It must be considered a potential vector,

as its restricted distribution coincides with the densely populated Natal coast.

Aedes simpsoni: Its similarity to *Ae. aegypti* in distribution and ecology strongly suggests that this species is a potential vector. *Aedes simpsoni* is common throughout the tropical and subtropical regions of South Africa (Table 1) and is highly prevalent throughout its range, utilizing natural and artificial larval niches in a variety of environments including the feral (tree holes), agricultural (commercial banana plantations) and domestic (Muspratt 1956, Huang 1986b). It is diurnally active (Muspratt 1956) and bites man readily (Table 3). North and East African records of its biting rate in human-baited collections and its vector competence are open to question after the taxonomic revision of the *Ae. simpsoni* group by Huang (1986a, 1986b). *Aedes simpsoni* was described as a major vector of yellow fever in Nigeria (Lee and Moore 1972), in Uganda (Gillett 1969) and in East Africa (Hamon et al. 1971), but Huang (1986b) suggests that this work relates to *Ae. bromeliae*; apparently *Ae. simpsoni* is confined to southern Africa.

Aedes strelitziae: The preferred oviposition site of this species is in the leaf axils of *Strelitzia nicolai*, a common plant on the Natal coast and in montane and riverine forests further inland (Muspratt 1956). This plant is much more prevalent than *Dracaena hookeriana*. Only in a few localities and at low abundance did *Ae. strelitziae* oviposit in bamboo pots (Table 1). Artificial containers were also used to some extent but only when associated with large stands of *Strelitzia nicolai*. This dependence on a particular plant introduces restrictions on geographic distribution, but *Ae. strelitziae* still exists in close proximity to large human populations on the Natal seaboard and is highly anthropophilic (Table 3).

Eretmapodites quinquevittatus: This species appeared to be the only member of the genus to occur in abundance in the study area. The oviposition requirements almost always involved small collections of rainwater in discarded tins and cardboard cartons (milk and local beer). Muspratt (1955) confirms these breeding requirements and indicates that natural collections of rainwater in fallen leaves, snail shells and leaf axils are also utilized. The facility with which the species utilizes such small receptacles is apparently augmented by its larval behavior, including the ability for facultative cannibalism and larval activity out of the water (Hopkins 1952), both of which were observed in our laboratory.

Some inconsistencies with respect to larval requirements and behavior exist in the litera-

ture. Lounibos (1980) found that *Er. subsimplicipes* is common in and *Er. quinquevittatus* absent from the fruit husks of the Loganiaceae in Kenya (Lounibos 1978, 1980). We found just the opposite with apparently monospecific collections of *Er. quinquevittatus* occurring in fruit husks of *Strychnos madagascariensis* at St. Lucia Estuary. With respect to larval predation, Hartberg and Gerberg (1971) report no evidence of cannibalism for the species in the laboratory, although Haddow (1946) describes larvae from Uganda as predatory. Lounibos (1980) suggests that, unlike *Er. silvestris* Ingram and de Meillon and *Er. subsimplicipes*, it is not able to develop beyond the third instar on a predatory diet alone.

In Natal, *Er. quinquevittatus* has become adapted to both natural and artificial small receptacles for its larval habitat. Furthermore, it is closely associated with man in the domestic environment, has a diurnal biting-activity pattern and is significantly anthropophilic. Consequently, it must be regarded as a potential vector of dengue.

It may be concluded that of the 7 species identified as potential vectors of dengue in South Africa, five are potentially epidemic vectors. The 5 species fall into 2 groups according to our ecological criteria for selection. The most important group comprises *Ae. aegypti*, *Ae. simpsoni* and *Er. quinquevittatus* because of the prevalence of these species and their close association with man in the urban environment. The second group consists of *Ae. demeilloni* and *Ae. strelitziae* which are regarded as less important because of their dependence on specific plants for their larval habitats, which limits their distribution. The 2 remaining species, *Ae. furcifer* and *Ae. cordellieri*, are essentially rural species limited to the tropical region. Therefore, although they are both probably competent vectors, they are unlikely to become involved in epidemic transmission.

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REFERENCES CITED

- Cordellier, R., B. Bouchité, J. C. Roche, N. Monteny, B. Diaco and P. Akoliba. 1983. Circulation selvatique du virus dengue 2 en 1980, dans les savanes sub-soudaniennes de Côte d'Ivoire. Données entomologiques et considérations épidémiologiques. Cah. O.R.S.T.O.M. Ser. Entomol. Med. Parasitol. 21:165-179.
- Edwards, F. W. 1941. Mosquitoes of the Ethiopian region. III. Culicine adults and pupae. Br. Mus. (Nat. Hist.), London.
- Gillett, J. D. 1969. Yellow fever (transmitted by *Aedes africanus* (Theo.) and *Ae. simpsoni* (Theo.) in Bwamba) in East Africa today. E. Afr. Med. J. 46:22-25.
- Gubler, D. J. 1988. Dengue, pp. 223-260. In : T. P. Monath (ed.), The arboviruses: epidemiology and ecology, Vol. 2. CRC Press, Boca Raton, FL.
- Haddow, A. J. 1946. The mosquitoes of Bwamba County, Uganda. IV. Studies on the genus *Eretmapodites*, Theobald. Bull. Entomol. Res. 37:57-82.
- Hamon, J., G. Pichon and M. Cornet. 1971. La transmission du virus amaril en Afrique occidentale. Ecologie, répartition, fréquence et contrôle des vecteurs, et observations concernant l'épidémiologie de la fièvre jaune. Cah. O.R.S.T.O.M. Ser. Entomol. Med. Parasitol. 9:3-60.
- Hartberg, W. K. and E. J. Gerberg. 1971. Laboratory colonization of *Aedes simpsoni* (Theobald) and *Eretmapodites quinquevittatus* Theobald. Bull. W.H.O. 45:850-852.
- Hopkins, G. H. E. 1952. Mosquitoes of the Ethiopian region. I. Larval bionomics of mosquitoes and taxonomy of culicine larvae. 2nd edition. Br. Mus. (Nat. Hist.), London.
- Horsfall, W. R. 1955. Mosquitoes. Their bionomics and relation to disease. Constable and Co. Ltd., London.
- Huang, Y. M. 1986a. Notes on the *Aedes (Diceromyia) furcifer* group, with a description of a new species (Diptera: Culicidae). Proc. Entomol. Soc. Wash. 88:634-649.
- Huang, Y. M. 1986b. *Aedes (Stegomyia) bromeliae* (Diptera: Culicidae), the yellow fever virus vector in East Africa. J. Med. Entomol. 23:196-200.
- Hunt, R. H., A. J. Cornel and M. Coetzee. 1990. *Aedes albopictus*: an unwelcome introduction to Cape Town. S. Afr. J. Epidemiol. Infect. 5:9-10.
- Jupp, P. G. 1980. Studies on *Aedes furcifer* and other mosquitoes in relation to their role as vectors of chikungunya virus in South Africa, pp. 37-38. Proc. 3rd Entomol. Congress Entomol. Soc. South Afr., Pretoria, September 16-18, 1980.
- Jupp, P. G. and B. M. McIntosh. 1988. Chikungunya virus disease, pp. 137-157. In : T. P. Monath (ed.), The arboviruses: epidemiology and ecology, Vol. 2. CRC Press, Boca Raton, FL.
- Jupp, P. G. and B. M. McIntosh. 1990. *Aedes furcifer* and other mosquitoes as vectors of chikungunya virus at Mica, northeastern Transvaal, South Africa. J. Am. Mosq. Control Assoc. 6:415-420.
- Jupp, P. G., A. Kemp and C. Frangos. The potential for dengue in South Africa: the taxonomic status of *Aedes aegypti* populations. (In manuscript).
- Knight, K. L. and A. Stone. 1977. A catalog of the mosquitoes of the world (Diptera: Culicidae), 2nd edition. Thomas Say Foundation, Vol. 6. Entomol. Soc. Am., College Park, MD.
- Lee, V. H. and D. L. Moore. 1972. Vectors of the 1969 yellow fever epidemic on the Jos Plateau, Nigeria. Bull. W.H.O. 46:669-673.
- Lounibos, L. P. 1978. Mosquito breeding and oviposition stimulant in fruit husks. Ecol. Entomol. 3:299-304.
- Lounibos, L. P. 1980. The bionomics of three sympatric *Eretmapodites* (Diptera: Culicidae) at the Kenya coast. Bull. Entomol. Res. 70:309-320.
- Lumsden, W. H. R. 1955. An epidemic of virus disease in Southern Province, Tanganyika Territory, in 1952-53. II. General description and epidemiology. Trans. R. Soc. Trop. Med. Hyg. 49:33-57.
- Lumsden, W. H. R. 1957. The activity cycle of *Aedes (Stegomyia) aegypti* (L.) (Dipt., Culicid.) in Southern Province, Tanganyika. Bull. Entomol. Res. 48:769-782.
- Mattingly, P. F. 1953. The sub-genus *Stegomyia* (Diptera: Culicidae) in the Ethiopian Region. II. Distribution of species confined to the East and South African sub-region. Bull. Br. Mus. (Nat. Hist.) Entomol. 3:1-65.
- McIntosh, B. M., P. G. Jupp and J. da Sousa. 1972. Mosquitoes feeding at two horizontal levels in gallery forest in Natal, South Africa, with reference to possible vectors of chikungunya virus. J. Entomol. Soc. South Afr. 35:81-90.
- McIntosh, B. M., P. G. Jupp and I. dos Santos. 1977. Rural epidemic of chikungunya in South Africa with involvement of *Aedes (Diceromyia) furcifer* (Edwards) and baboons. S. Afr. J. Sci. 73:267-269.
- Muspratt, J. 1955. Research on South African Culicini (Diptera: Culicidae). III. A check-list of the species and their distribution, with notes on taxonomy, bionomics and identification. J. Entomol. Soc. South Afr. 18: 149-207.
- Muspratt, J. 1956. The *Stegomyia* mosquitoes of South Africa and some neighbouring territories. Mem. Entomol. Soc. South Afr. 4.
- Port, G. R. and T. J. Wilkes. 1979. *Aedes (Diceromyia) furcifer/taylori* and a yellow fever outbreak in The Gambia. Trans. R. Soc. Trop. Med. Hyg. 73:341-344.
- Reinert, J. F. 1986. *Albuginosus*, a new subgenus of *Aedes* Meigen (Diptera: Culicidae) described from the Afrotropical region. Mosq. Syst. 18:307-326.
- Roche, J. C., R. Cordellier, J. P. Hervy, J. P. Digoutte and N. Monteny. 1983. Isolement de 96 souches de

- virus dengue 2 à partir de moustiques capturés en Côte-d'Ivoire et Haute-Volta. Ann. Virol. (Inst. Pasteur) 134E:233-244.
- Teesdale, C. 1959. Observations on the mosquito fauna of Mombasa. Bull. Entomol. Res. 50:191-208.
- Trpis, M., G. A. H. McClelland, J. D. Gillett, C. Teesdale and T. R. Rao. 1973. Diel periodicity in the landing of *Aedes aegypti* on man. Bull. W.H.O. 48:623-629.
- Ward, R. A. 1984. Second supplement to "A catalog of the mosquitoes of the world" (Diptera: Culicidae). Mosq. Syst. 16:227-270.