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Dispersal and survival of *Anopheles funestus* and *A. gambiae* s.l. (Diptera: Culicidae) during the rainy season in southeast Tanzania

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Abstract

In a rural area of south~~western~~ Tanzania, studies were undertaken on the dispersal and survival of *Anopheles funestus* Giles and *A. gambiae* Giles *s.l.* during the rainy season. Blood fed, resting mosquitoes were collected ~~out~~doors, marked with fluorescent powder and released on the same day from two different sites in the study area. For two weeks indoor resting mosquitoes were collected from 11 houses in the release area. Additional collections were made with a light trap from a sentinel house in the centre of the study area. *Anopheles funestus* was more abundant than *A. gambiae* s.l. Of 4262 *A. funestus* and 645 *A. gambiae* s.l. released, 4.3% and 7.4%, respectively, were recaptured. Dispersal of mosquitoes was not random: one of three areas was favoured significantly more than the other areas, as shown by the recapture and movement rates of marked mosquitoes. Based on the regression of the recapture rate, estimated daily survival rates of *A. funestus* and *A. gambiae* s.l. were 0.63 and 0.78, respectively. These were significantly different. The differences in dispersal and survival rates between the two species are discussed in view of local topography and species-specific characteristics.

Introduction

In order to improve our understanding of malaria epidemiology and malaria risk, information about the distribution and survival of the vectors is required. If there is homogeneous mixing of the vector population, then mosquito density is the only factor determining the rate of transmission to the human population (Smith *et al.*, 1993). If the distribution of the insects is not homogeneous, then this is not the case. The homogeneity of the vector distribution is likely to be dependent on dispersal, which in turn may be influenced by the relationship between breeding and feeding sites (Smith *et al.*, 1995; Ribeiro *et al.*, 1996). The main African vectors, *Anopheles funestus* Giles and *A. gambiae* s.s. Giles (Diptera: Culicidae), are highly synanthropic. Both are anthropophagic and endophilic (Gillies & De Meillon, 1968). Larvae of *A. funestus* occur in semi-permanent water collections and are often associated with rice fields, whereas *A. gambiae* s.s breeds in small temporary water collections such as puddles. The other major vector, *A. arabiensis* Patton (Diptera: Culicidae), a sibling of *A. gambiae* s.s, also breeds in temporary pools but is less anthropophilic and will feed on animals when they are available. In villages where alternative hosts are not available, *A. arabiensis* feeds on man and is

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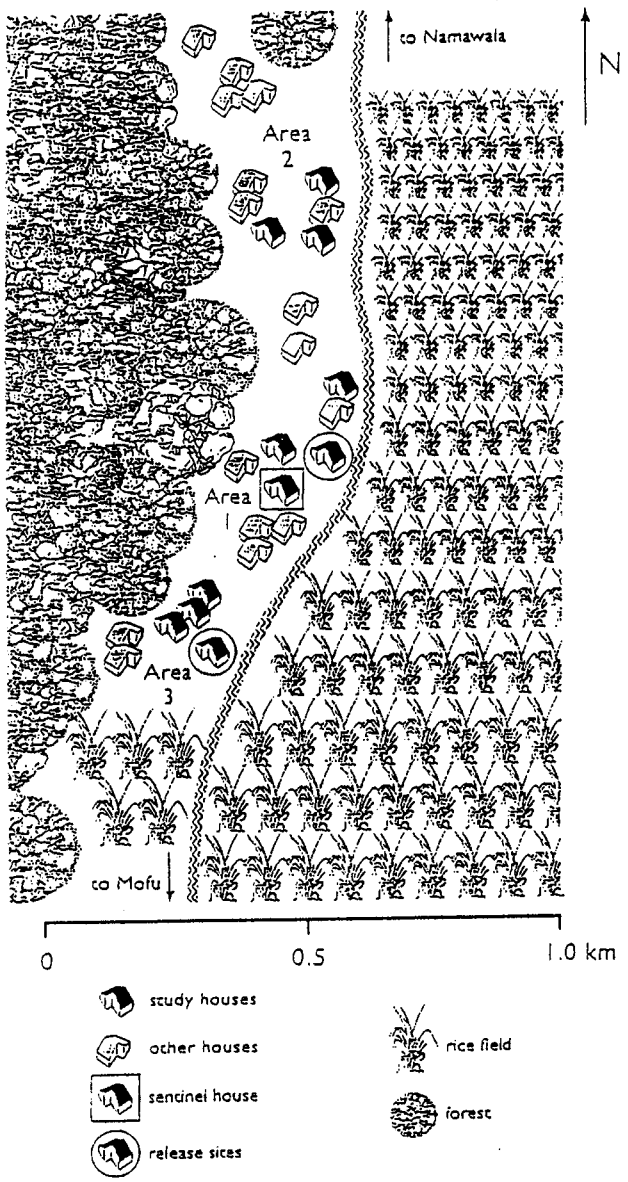

Fig. 1. Map of the study area, near Namawala, Tanzania.

as endophilic as *A. gambiae*. This is the case in the Kilombero valley of Tanzania during the wet season (Charlwood *et al.*, 1995a), an area where all three vectors are common.

The most suitable way of directly determining the relative amount of homogeneity in a mosquito population is by capture–recapture experiments (Service, 1993). This also provides estimates of survival rates, which directly affect vectorial capacity. A series of capture–recapture experiments were therefore undertaken in an isolated hamlet in the Kilombero valley where malaria transmission is intense. In order to validate the results obtained, alternative techniques such as age determination by dissection were also applied.

Materials and methods

The study was conducted in Kikulukutu, a small hamlet of Namawala village, approximately 40 km west of Ifakara, in the Kilombero Valley of Tanzania. At the time of the study (May 1990), some 60 people lived in Kikulukutu in 15 households (fig. 1). The hamlet consisted of mud walled and thatched roofed farm houses that allowed easy access to mosquitoes. Houses were situated mostly on the western side of a motorable track. They were built on small hillocks which remained dry at times of excessively heavy rainfall. The study area was divided into three sub-areas (area 1, 2 and 3, each 0.5 km apart (fig. 1). In sub-area 1, houses were grouped close together. In the other areas they were more widely separated. To the east and south, Kikulukutu was bordered by a very large wet-season swamp (part of the Kilombero river flood plain), which was used for rice cultivation. To the west and north there was a natural stand of Miombo woodland. Villagers used the slash-and-burn method of agriculture, and most fields were of a temporary nature. In the rainy season wild animals such as buffalo, bushpig and warthog often competed with the villagers for the crops.

From the 5th to the 17th May 1990 resting mosquitoes were collected between 8.00 and 10.00 am with aspirators from four houses each in area 1 and 3, respectively, while in area 2 three houses were sampled. One isolated house,

Table 1. Recaptures of marked *Anopheles funestus* and *A. gambiae* s.l. over time.

Day	Species	Marking colour: Yellow	Red	Orange	Pink	Total (%)
Total released						
	Ag	140	128	181	196	645
	Af	939	840	1191	1292	4262
Recaptures per day						
1	Ag	*	2	6	1	9
	Af	*	21	12	13	46
2	Ag	2	3	3	4	12
	Af	19	16	8	9	52
3	Ag	2	1	3	3	9
	Af	17	10	7	4	38
4	Ag	1	1	1	3	6
	Af	6	1	2	8	17
5	Ag	3	2	0	0	5
	Af	6	2	1	1	10**
6	Ag	1	0	1	0	2
	Af	2	0	1	7	10
7	Ag	2	0	0	0	2
	Af	5	3	1	2	11
8	Ag	1	1	0	0	2
	Af	0	0	0	0	0
9	Ag	0	0	0	0	0
	Af	0	0	0	0	0
10	Ag	1	0	0	0	1
	Af	0	0	0	0	0
11	Ag	0	0	0	0	0
	Af	0	0	0	0	0
Total recaptured						
	Ag	13(9.2%)	10(7.8%)	14(7.7%)	11(5.6%)	48(7.4%)
	Af	55(5.8%)	53(6.6%)	32(2.6%)	44(3.4%)	184(4.3%)

Af, *A. funestus*; Ag, *A. gambiae*.
* No collections were made on the first day after release of yellow marked mosquitoes.
** One mosquito collected in an isolated house 0.5 km south-east of sub-area 3.

1 km south-east of area 3, was also sampled. In the study area resting collections of anopheline mosquitoes exist only of *A. funestus* and *A. gambiae* s.l., all other anopheline species being exophilic and exophagic. For the releases, mosquitoes were counted, transferred to 15 cm cubic cages and marked with fluorescent powder (Dayglow®). This was done by placing the mosquito cage inside a plastic bag and blowing a small quantity of powder into the cage from a syringe. Mosquitoes became well covered with the powder without showing a negative effect of the treatment. Immediately after marking, the cage was opened underneath the veranda of a house in area 1 or area 3 and were allowed to leave undisturbed. On release, most of the mosquitoes flew into the roof of the house and less than 5% of the insects remained in the holding cage. Different colours were used for each release (table 1).

An estimate of the ratio of *A. funestus* and *A. gambiae* s.l. was obtained from resting collections made in the four days prior to and following release. The mean of the previous four days collection was used to calculate the number of marked mosquitoes released.

Resting mosquitoes were collected daily from 11 houses for approximately two weeks following each release. A CDC miniature light trap within another sentinel house (fig. 1) was also run on a daily basis. Data from this trap provided information on the endophilic mosquito population in the study area for the succeeding two years (Smith *et al.*, 1993; Charlwood *et al.*, 1995b). Collected mosquitoes were examined with an ultraviolet light for the presence of marks. A proportion of the light trap collections was dissected to determine the gonotrophic age.

The daily survival rate of the mosquito population was calculated by transforming the daily recaptures of marked mosquitoes to natural logarithms (N + 1) and regressing this data over time. Because most of the mosquitoes were blood fed and unlikely to return to feed within one day of release, recapture data from day 1 after release were excluded from the calculations. The antilog of the slope of regression was used to estimate survivorship (Gillies, 1961). Unless otherwise mentioned, analyses of variance and the Kruskal-Wallace test were used for statistical calculations (Sokal & Rohlf, 1969).

Results

Resting collections

A total of 27,470 *A. funestus* and 7040 *A. gambiae* s.l. females were obtained from resting collections during the study period. These consisted almost exclusively of female blood fed *A. funestus* and *A. gambiae* s.l. In several instances, the number of mosquitoes collected from a single house was in excess of 900 mosquitoes.

The mean density of *A. funestus* per house in area 2 was always lower than that of the mean density per house in areas 1 and 3. This difference was significant for all but three of the collection days ($P < 0.05$) (fig. 2). During the recapture experiments, the numbers of *A. funestus* in both resting and light trap collections declined, however they increased towards the end of the month (fig. 3).

Mean densities of *A. gambiae* s.l. per house were similar in all areas (fig. 2). Towards the end of the study, the *A. gambiae* s.l. population increased in all areas.

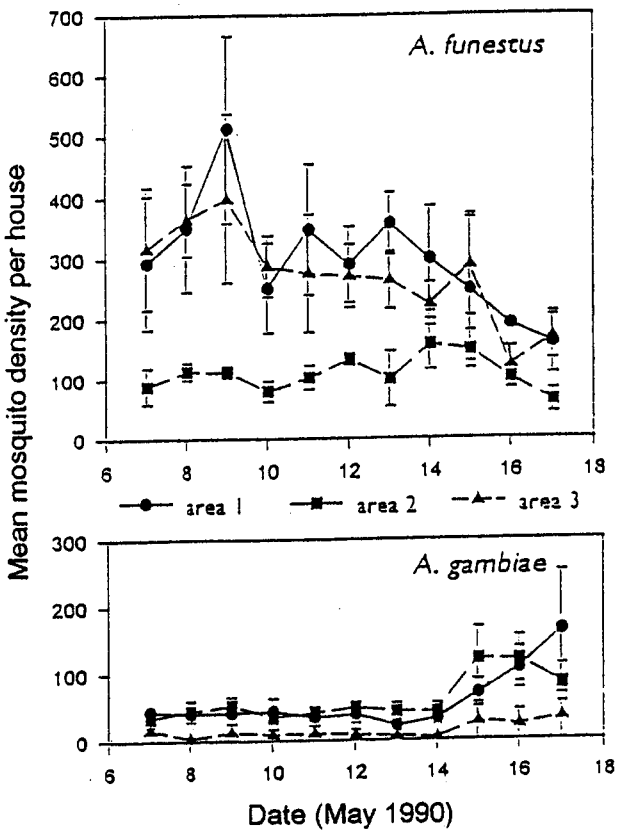

Fig. 2. Average density, expressed as geometric mean per house, of female *Anopheles funestus* and *A. gambiae* s.l. in three sub-areas based on resting catches. Vertical bars represent standard errors.

Light trap collections

Four thousand five hundred and fourteen *A. funestus* and 4061 *A. gambiae* s.l. were collected in the light trap between May 7 and 17. The parity rate of 524 *A. funestus* and 653 *A. gambiae* were determined (mean number dissected per day being 40 and 59, respectively). As in the resting catches, the number of *A. funestus* collected declined in the first two weeks of May, parity rate decreased and the population increased from the middle of the month (fig. 3). Numbers of *A. gambiae* in the light trap rose from 78 on 13 May to 1591 four days later. The relationship between the number of mosquitoes caught in the light trap and the numbers biting varies from 0.67 (Lines *et al.*, 1991) to 1.23 (Davis *et al.*, 1995). Using these conversion factors, estimated numbers biting at peak densities varied between 1298 and 2374 per person per night. The number returned to previous levels within four days after the peak (fig. 3). On 13 May, 91% (52/57) *A. gambiae* dissected were parous whereas four days later 31 (26%) were pregravid (with ovaries at Christophers stage I); 46 (39%) were nulliparous (with ovaries at Stage II) and only two (1.7%) were parous. Hence the great majority of the mosquitoes on that date consisted largely of newly emerged insects. The pronounced peak observed in the light trap collections was not evident in the resting collections where numbers rose more slowly (fig. 2).

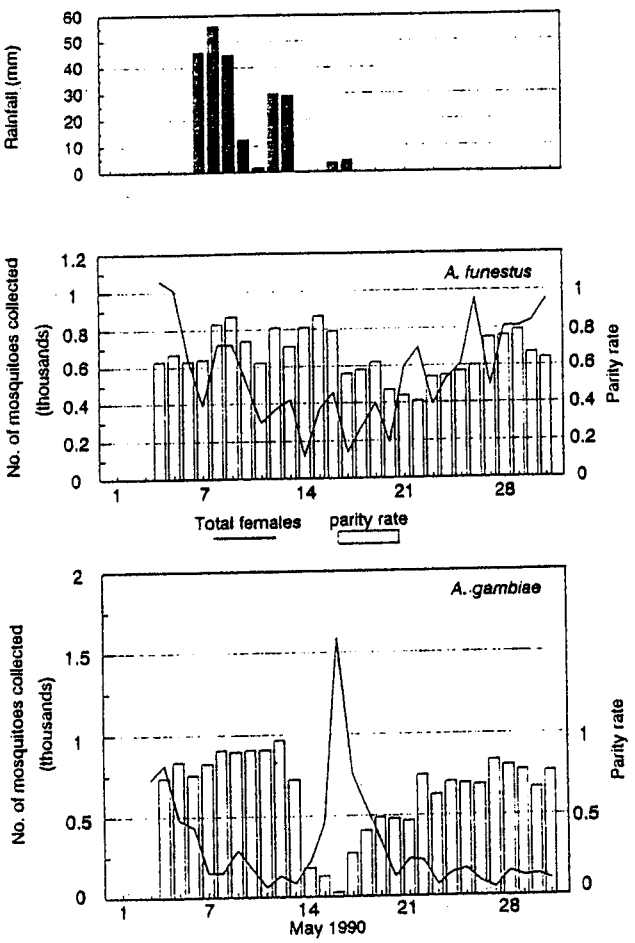

Fig. 3. Daily rainfall and number of female *Anopheles funestus* and *A. gambiae* s.l. collected by light trap in the sentinel house in May 1990. The mark–recapture study was conducted between May 5 and 17, with releases on May 5 and 6. The proportion of parous females is presented in bars.

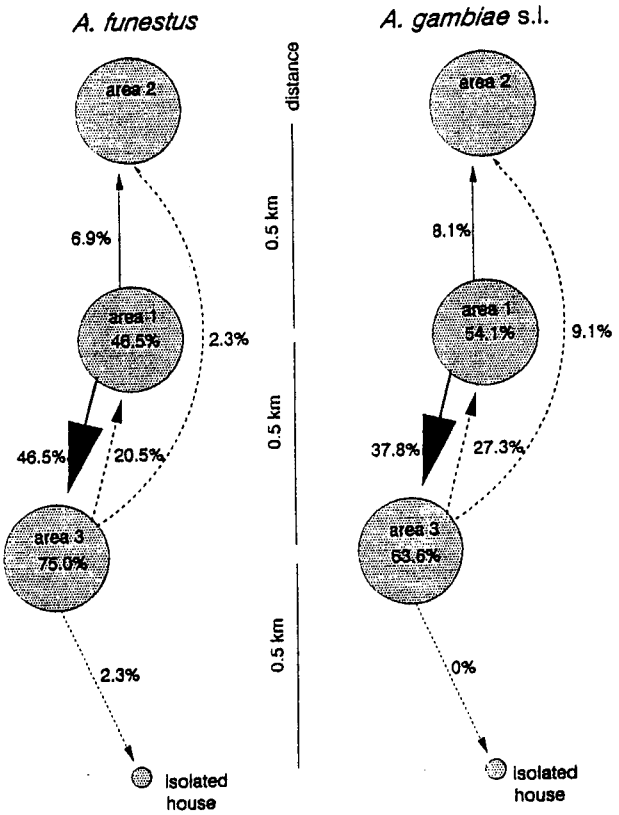

Fig. 4. Recaptures and dispersal of marked mosquitoes over the study area. Solid arrows: mosquitoes released in area 1. Broken arrows: mosquitoes released in area 3.

Capture–recapture experiments

A total of 4262 *A. funestus* and 645 *A. gambiae* s.l. were released on four separate occasions over two days, and respectively 184 and 48 recaptured over the subsequent ten days (table1). The overall recapture rate of *A. funestus* was therefore 4.3% and of *A. gambiae* s.l. 7.4%. The nutritional and reproductive condition of 142 *A. funestus* and 30 *A. gambiae* s.l. recaptured resting was determined; 35.2% and 16.7%, respectively, were gravid, the remainder were blood fed. The parity rate of released insects determined from a sample dissected on the day of release, was estimated at 67–75%. All mosquitoes recaptured three days after release were parous.

Seventy five percent of *A. funestus* and 64% of *A. gambiae* recaptured in area 3, had been released there. The percentage of mosquitoes released and recaptured in area 1 was considerably lower, being 47 and 54%, respectively. Figure 4 illustrates the dispersal of the species between the study areas. Although the distances between the study areas were similar (fig. 1), overall dispersal from the central area 1 occurred more to area 3 than to area 2 in both species. The proportion of *A. funestus* that moved from area 1 to area 3 was significantly greater than that which moved from area 3 to area 1 (Fisher exact test, $P < 0.005$). There was therefore a net dispersal of *A. funestus* in favour of area 3. This was not the case with *A. gambiae*, where the dispersal rates between the two areas were not significantly different. Area 2 was more favoured by *A. gambiae* than by *A. funestus*, but the data were too few for statistical comparison. In an isolated house, 0.5 km from sub-area 3, one marked *A. funestus* was collected among daily collections made for a different study (fig. 4). This mosquito had been released five days earlier in sub-area 3. Two *A. gambiae*, released in area 1, were serendipitously recaptured from Namawala village, 3 km north east of the study area, in an *ad hoc* collection.

Although the decline in recapture rate of *A. gambiae* was relatively consistent for the 12 days after release, the number of recaptured *A. funestus* showed a dramatic reduction on day 8 (fig. 5). This was reflected in estimates of the survival rate, which were 0.78 and 0.63 ($P < 0.005$). Survival rates of *A. funestus* at 0.73 remained significantly lower than that of *A. gambiae* even if the data from only days 2–7 are used in the analysis ($P < 0.05$). Estimated survival rates of mosquitoes recaptured in their areas of release were always higher than overall estimates (table 2) because recaptures of mosquitoes that had dispersed from the point of release were concentrated in the first few days after release.

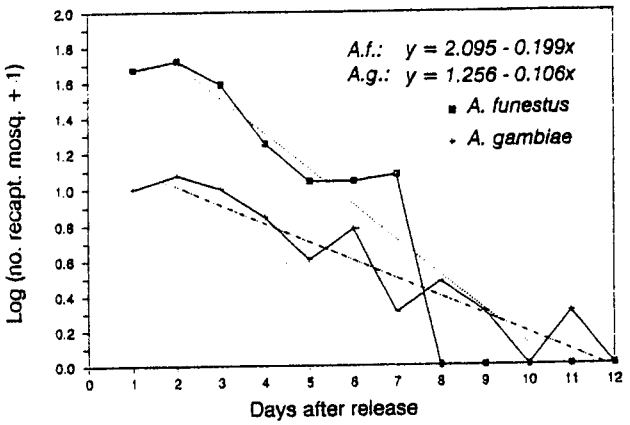

Fig. 5. The logarithm of the number of marked *Anopheles funestus* (■) and *A. gambiae* s.l. (+) collected over 12 days following release and the estimated regression. Combined collections of 11 resting catches and one light trap.

Table 2. Estimates of survival rates of *Anopheles funestus* and *A. gambiae* s.l. per study area and of all areas combined.

Recapture area	Origin of recaptured mosquitoes	Regression	Daily survival[1]
Anopheles funestus			
Area 1	Area 1	y = 1.491–0.135x	p = 0.733
	All releases combined	y = 1.565–0.140x	p = 0.725
Area 3	Area 3	y = 0.919–0.091x	p = 0.812
	All releases combined	y = 1.622–0.152x	p = 0.706
All areas combined	All releases combined	y = 2.095–0.199x	p = 0.632
Anopheles gambiae			
Area 1	Area 1	y = 0.791–0.068x	p = 0.856
	All releases combined	y = 0.897–0.079x	p = 0.833
Area 3	Area 3	y = 0.495–0.052x	p = 0.887
	All releases combined	y = 0.924–0.087x	p = 0.819
All areas combined	All releases combined	y = 1.256–0.106x	p = 0.783

[1] Antilog slope regression line (recaptures – day one) (Gillies, 1961).

Discussion

Both *A. gambiae* s.s. and *A. arabiensis* occur in the study area and fluctuations in relative proportions of the two species can be quite rapid (P. Luttikhuizen, personal communication), so one of the drawbacks of the present study is that the members of the *A. gambiae* complex were not identified to species. Nevertheless, the very rapid and marked rise in numbers caught in the light trap in the days around May 17 implies that a single species was present. It is well known that populations of *A. gambiae* s.l. can increase extraordinarily rapidly as breeding sites become available during the rainy season (Gillies & De Meillon, 1968). Therefore, the 20-fold increase in numbers caught in the light trap in a matter of days is not exceptional. The equally rapid drop in numbers is, however, unusual and can only have been due either to extreme mortality in the young mosquitoes or to emigration from the area. In a previous study density of mosquitoes did not affect feeding success and therefore survival (Charlwood *et al.*, 1995b) and in the present study >900 blood-fed *A. funestus* were caught from a single house on several occasions. In other species, mass emergence is associated with subsequent migration (Provost, 1952; Nielsen, 1958; White, 1970). Although we cannot distinguish between these two effects, we suggest that emigration was responsible for the drop in numbers.

Numbers of *A. gambiae* in the resting catches increased simultaneously with the rise observed in the light trap but the extent of the increase was markedly lower. Therefore, although the young mosquitoes readily entered houses, they did not appear to stay in them. This means that light trap and resting collections are likely to sample different fractions of the mosquito population and this should be considered in sampling procedures.

Migration out of the study area is unlikely to have been responsible for the sudden drop in the number of marked *A. funestus* caught six days after release. Since in other studies the survival rate of this species was similar to that of *A. gambiae* (Gillies & Wilkes, 1965; Charlwood *et al.*, 1995b; 1997), and since the proportion infected with sporozoites is similar (Charlwood *et al.*, 1997) it is unlikely that the real survival rate is as low as that estimated in the present study. Marking may reduce insect survival (Burkot *et al.*, 1990) and thus have adversely affected *A. funestus* more than *A. gambiae* because of its smaller size. However, the survival rates of *A. gambiae* were remarkably similar to those obtained with other methods (Gillies & Wilkes, 1965; Charlwood *et al.*, 1995b; 1997) and hence marking would not appear to have adversely affected *A. gambiae*. A more likely explanation is the disappearance of the marking powder on *A. funestus*, where due to small size of the mosquito, the marks become difficult to see over time.

The species ratio of unmarked mosquitoes collected in the eight days following release varied from 3.81 to 6.05 per day, with an average value of 5.04, *A. funestus* being the dominant species. We did not find this variation large enough to attach significance to differences between the numbers of *A. funestus* and *A. gambiae* recaptured, even though the recapture rate of the former was lower than that of the latter species.

Fewer mosquitoes of either species moved from area 1 into area 2 compared to movement from area 1 to area 3 and more mosquitoes remained in area 3 when they were released there than remained in area 1. Houses in area 3 were surrounded by flooded rice fields and it is probable that the availability of potential oviposition sites affected the distribution of the mosquitoes (Smith *et al.*, 1995; Thompson *et al.*, 1995; Ribiero *et al.*, 1996). This behaviour was more pronounced in *A. funestus* than in *A. gambiae* which reflects the known differences in preference for breeding sites. Distribution of hosts may also affect dispersal in these species (Gillies, 1961). The differential dispersal of the two vectors may have implications for the interpretation of malaria epidemiology.

It is concluded that in the study area *A. funestus* and *A. gambiae* dispersed differently in relation to the distribution of breeding sides, the former staying in or moving into an area with large bodies of standing water significantly more than the latter. *A gambiae* s.l. had a higher survival rate than *A. funestus*, possibly due to a disappearance of marked *A. funestus* eight days after release.

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*Sadly, Simon Sama died in May 1998.

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