Medical and Veterinary Entomology (1996) **10**, 203–219

Density, survival and dispersal of *Anopheles gambiae* complex mosquitoes in a West African Sudan savanna village

CARLO COSTANTINI,[1] SONG-GANG LI,[2,3] ALESSANDRA DELLA TORRE,[1] N'FALÉ SAGNON,[4] MARIO COLUZZI[1] and CHARLES E. TAYLOR[3] [1]Istituto di Parassitologia* and Fondazione Pasteur–Cenci Bolognetti, Università 'La Sapienza', Rome, Italy, [2]Department of Biology, Peking University, Beijing, China, [3]Department of Biology, University of California, Los Angeles, U.S.A., and [4]Centre National de Lutte contre le Paludisme, Ouagadougou, Burkina Faso

Abstract. To obtain information on adult populations of Afrotropical malaria vector mosquitoes, mark–release–recapture experiments were performed with *Anopheles* females collected from indoor resting-sites in a savanna area near Ouagadougou, Burkina Faso, during September 1991 and 1992. Results were used to estimate the absolute population densities, daily survival rates, and dispersal parameters of malaria vectors in that area.

In 1991 a total of 7260 female *Anopheles* were marked and released, of which 106 were recaptured in the release village and 6 in the neighbouring villages, a total recapture rate of 1.5%. The following year 13,854 female *Anopheles* were released and 116 recaptured in Goundri and 8 in the neighbouring villages, a total recapture rate of 0.9%. Recaptures were found in three of eight villages near Goundri. Nearly all of the recaptured mosquitoes were *An.gambiae s.l.* Of these, molecular determination revealed that *An.gambiae s.s.* and *An.arabiensis* were present in a ratio of ~2:3.

Two simple random models of dispersal were simulated and the parameters of the models determined by searching for the least-squared fit between simulated and observed distributions. The mean distance moved by individual mosquitoes, estimated in this way, ranged 350–650 m day^{-1}, depending on the model and the year considered. Population densities were estimated using the Lincoln Index, Fisher-Ford and Jolly's methods. The estimates of population size had high standard errors and were not particularly consistent. A 'consensus' value of 150,000–350,000 mosquitoes is believed to apply for the *An.gambiae s.l.* female population. Survival was estimated to be 80–88% per day.

Key words. *An.arabiensis, An.funestus, An.gambiae,* Culicidae, mark–release–recapture, population size, survival, dispersal, dispersion, computer simulation, Burkina Faso, Sudan savanna vegetation belt, West Africa.

Introduction

Mark–release–recapture (MRR) procedures are often used to investigate mosquito populations. Service (1993) lists more than 150 such studies, including several with malaria vector species of the Afrotropical *Anopheles gambiae* Giles complex. For example, in Tanzania Gillies (1961) estimated that laboratory-reared *An.gambiae* males and females moved over 1 km, on average, before recapture during the next few weeks, and that their dispersal was non-random, related closely to the distribution of human habitations. *An.gambiae* mortality was estimated to be 16% per day. In the same area, for both *An.gambiae* and *An.funestus* Giles, MRR samples collected indoors and outdoors showed no significant tendency to repeated endophily or exophily (Lines *et al.*, 1986).

Anopheles gambiae sensu lato (*s.l.*) comprises multiple sibling species and chromosomal forms that differ in various ways (Coluzzi *et al.*, 1979, 1985). Population densities vary drama-

*W.H.O. Collaborating Centre for Malaria Epidemiology.

Correspondence: Dott. Carlo Costantini, Department of Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, U.K.

tically from place to place, and effective population sizes are thought to differ by several orders of magnitude (Taylor *et al.*, 1993). To counteract the tremendous vector potential of the *Anopheles gambiae* complex it has been suggested that refractory strains, incapable of transmitting malaria, might be genetically engineered and released to displace conspecific indigenous vector populations (W.H.O., 1991; Collins, 1994; Curtis, 1994). Such a programme requires much specific information on anopheline population structure and dynamics, dispersal and bionomics (Coluzzi, 1992; Collins & Besansky, 1994). Local knowledge about flight range and the rate of interchange between vector populations of adjacent areas is also desired for conventional vector control programmes, and for understanding the degree of parasite panmixia (particularly of *Plasmodium falciparum*) via the mosquito vector (Gupta & Day, 1994). Information obtained from MRR studies contributes to that knowledge.

There is a need to explore new and possibly better ways to analyse mosquito dispersal. Statistical analysis of MRR experiments has been very sensitive to small departures from assumptions in the model. In particular, when sampling is not uniform over the area of dispersal – or when the farthest dispersers are not included – then the estimates are likely to be wrong (Dobzhansky & Wright, 1943). This is especially important for mosquitoes, where samples are taken only from human habitations, which are typically arranged non-uniformly. For the analysis below, we attempt to describe mosquito dispersal by several models, then estimate the parameters in those models by minimizing the difference between observed distributions and those simulated on a computer. This procedure was first used to estimate dispersal by Dobzhansky *et al.* (1979) and by Taylor *et al.* (1987) for *Drosophila*. Though computationally demanding, the method enables estimation of active dispersal that would not be possible by ordinary means. Our analysis is based on a series of MRR experiments with two species of the *Anopheles gambiae* complex: *An.arabiensis* Patton and *An.gambiae* Giles *sensu stricto* (*s.s.*), conducted over a 2-year period near Ouagadougou, Burkina Faso. The primary objective was to gain a better understanding of dispersal in this species group and to begin development of a computer model for their behaviour.

Study area

MRR experiment were performed in September 1991 and 1992 at Goundri (12°30′N, 1°20′W), a small village located 35 km north-east of Ouagadougou, Burkina Faso, between Loumbila and Ziniaré. This is largely an agricultural region in the Sudan savanna vegetation belt of Western Africa (see Lawson, 1966). Millet and sorghum are the main crops; rice and vegetables are cultivated where permanent water is available. Mean rainfall is *c.* 800 mm/year (with 20% variability between different years) falling mainly in June–September, when the temperature ranges from ~22°C to ~32°C (mean 26–27°C), with mean relative humidity (RH) 60–75%. The rest of the year is typically dry (<20% of annual rainfall; mean RH 20–60%), with mean temperature reaching 32°C (data from ASECNA, Burkina Faso (E.D.S., 1967)).

In September 1991 rainfall was 48 mm, compared to a monthly mean of 127 mm. The wind blew during the nights, typically from SSW (mean vector angle 213°), with a mean speed of 1.41 m s^{-1}. During the experiment in September 1992, rainfall was 45 mm, following a period of heavy showers (250 mm in 1 week); the mean wind speed and direction were respectively 0.99 m s^{-1} and SSW 200° (data from ASECNA, Burkina Faso).

Maps of the collecting region are shown in Figs 1 and 2. Goundri comprises a cluster of about eighty compounds dispersed over approximately 4 km^2. Each compound is a family unit, consisting of two to twelve small mud huts. The huts may be round (*c.* 3 m diameter) with thatched roofs ('Mossi' type), or rectangular (*c.* 3 × 6 m) with corrugated iron roofs ('Bobo' type). Approximately 800 people of the Mossi ethnic group live in Goundri. Near the village are two major sources of mosquitoes: an artificial lake of permanent water about 500 m from the village edge, and a clay quarry with semi-permanent water about 200 m from the nearest compound.

Extra collections were made from huts in nearby (1–4 km away) Mossi villages of Nangtenga, Sa, Tanlarogo, Tanguen, Managsombo, Bagaren and Kamsaoguen, and one of two small villages of the Peul (Fulani) ethnic group. Goundri has been studied for many years in conjunction with the Centre National de Lutte contre le Paludisme, a joint Burkinabé–Italian health-aid and research programme in Ouagadougou. Consequently there is a body of useful data on the species of mosquitoes there (cf. Hamon, 1963; Hamon *et al.*, 1966), their feeding habits and the epidemiology of malaria in the region (Merzagora, 1993). It is noteworthy that Goundri is at precisely the same latitude (12°30′N) as the Garki Project area, 1200 km to the east (9°E) in Nigeria, where the epidemiology of malaria and the impact of insecticidal house-spraying have been investigated most comprehensively (Molineaux & Gramiccia, 1980), under similar ecological circumstances.

Three vectors of malaria are present in the Goundri area: *An.arabiensis, An.gambiae, s.s.* and *An.funestus*. Other species occasionally found inside dwellings are *An.rufipes* (Gough), *An.pharoensis* Theobald, *An.ziemanni* Grünberg, *Mansonia uniformis* (Theobald), *Ma.africana* (Theobald), and *Culex quinquefasciatus* Say. Two chromosomal 'forms' (potential incipient species) of *An.gambiae s.s.* are found in Goundri – 'Mopti' and 'Savanna' (Coluzzi *et al.*, 1985) – with 'Mopti' karyotypes generally predominant. *An.arabiensis* populations have considerable chromosomal inversion polymorphism, but no chromosomal 'forms' have been recognized (Petrarca *et al.*, 1986). During our study it was not possible to distinguish routinely between the chromosomal forms of *An.gambiae s.s.*, though for some 1992 samples the sibling species of the *An.gambiae* complex were identified by means of PCR molecular probes (Paskewitz & Collins, 1990; Scott *et al.*, 1993). From pyrethrum spray collections (PSC) indoors at Goundri on 14 September the species ratio of females was 118 *An.gambiae* to 100 *An.arabiensis*, and on 23 September was 56:83. Therefore we take the ratio *arabiensis:gambiae* to be around 1:1, although this varied during the experiment ($G = 6.54$; d.f. = 1; $P = 0.01$). Similar relative frequencies of these two members of the *An.gambiae* complex have been found at Goundri in previous years at this season (Merzagora, 1993).

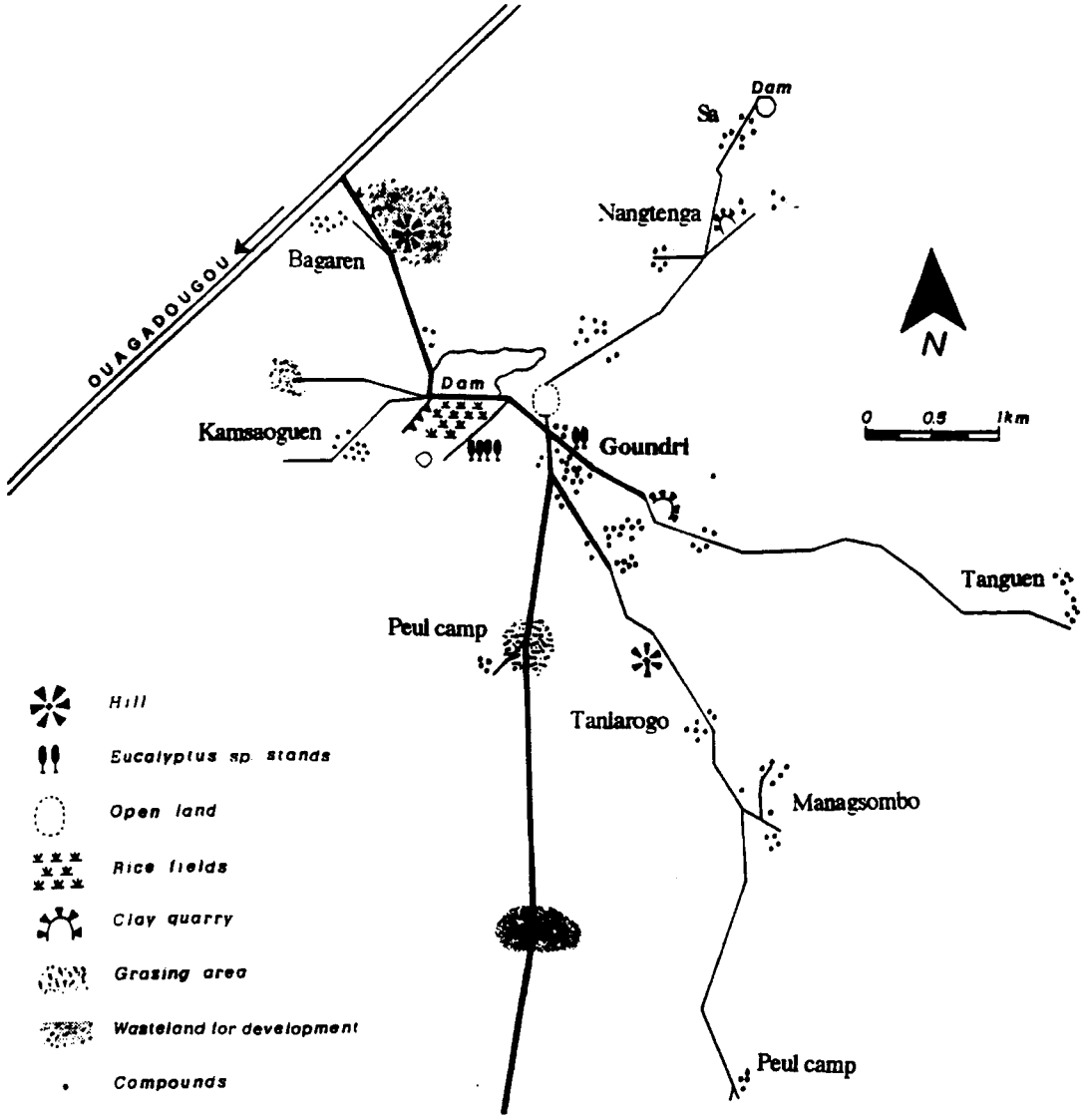


Fig. 1. Sketch map of the study area, showing Goundri and neighbouring villages. Mosquito collections were made in all villages shown on the map, except the Peul (Fulani) camp to the south-south-east.

Materials and Methods

All releases were made in Goundri with mosquitoes that had been hand-collected at 09.00–12.00 hours from indoor resting-sites in that village. Subsequent recaptures were made, either by hand-collection or PSC indoors, at Goundri and the neighbouring villages shown in Figs 1 and 2. By the efforts of five to ten (usually eight) collectors, it was possible to sample 50–85 huts per day with hand-catches or 25–35 huts per day with PSC procedures as described by Service (1993). In each year there were five releases, with a separate colour used to mark each batch released and eleven recaptures. The date, procedure and location of each collection are shown in Table 1. To avoid possible lingering insecticidal or deterrent effects of PSCs, collections were not repeated in the same hut until 5–7 days had elapsed after each PSC. Indoor-resting mosquitoes were collected alive into paper cups by means of electric aspirators based on the design of Coluzzi & Petrarca (1973).

In 1991 we tried to collect only female anophelines by aspiration into paper cups, lined with black cotton, where they were illuminated with a portable UV lamp to detect any mosquitoes that had been marked earlier. After transfer to a cage for day-time storage, they were aspirated into paper cups which had been lightly dusted with a day-specific coloured fluorescent powder. They were then put into a release cage, and kept humid with a moist towel until release. The powders for dusting were 'Day-Glo' A- and AX-series thermoplastic fluorescent pigments: Aurora Pink, Blaze Orange, Saturn Yellow, Signal Green and Horizon Blue, donated by Day-Glo Color Co. (Cleveland, Ohio, U.S.A.). This procedure enabled scoring marked mosquitoes and the release of newly marked mosquitoes at the same time. PSCs

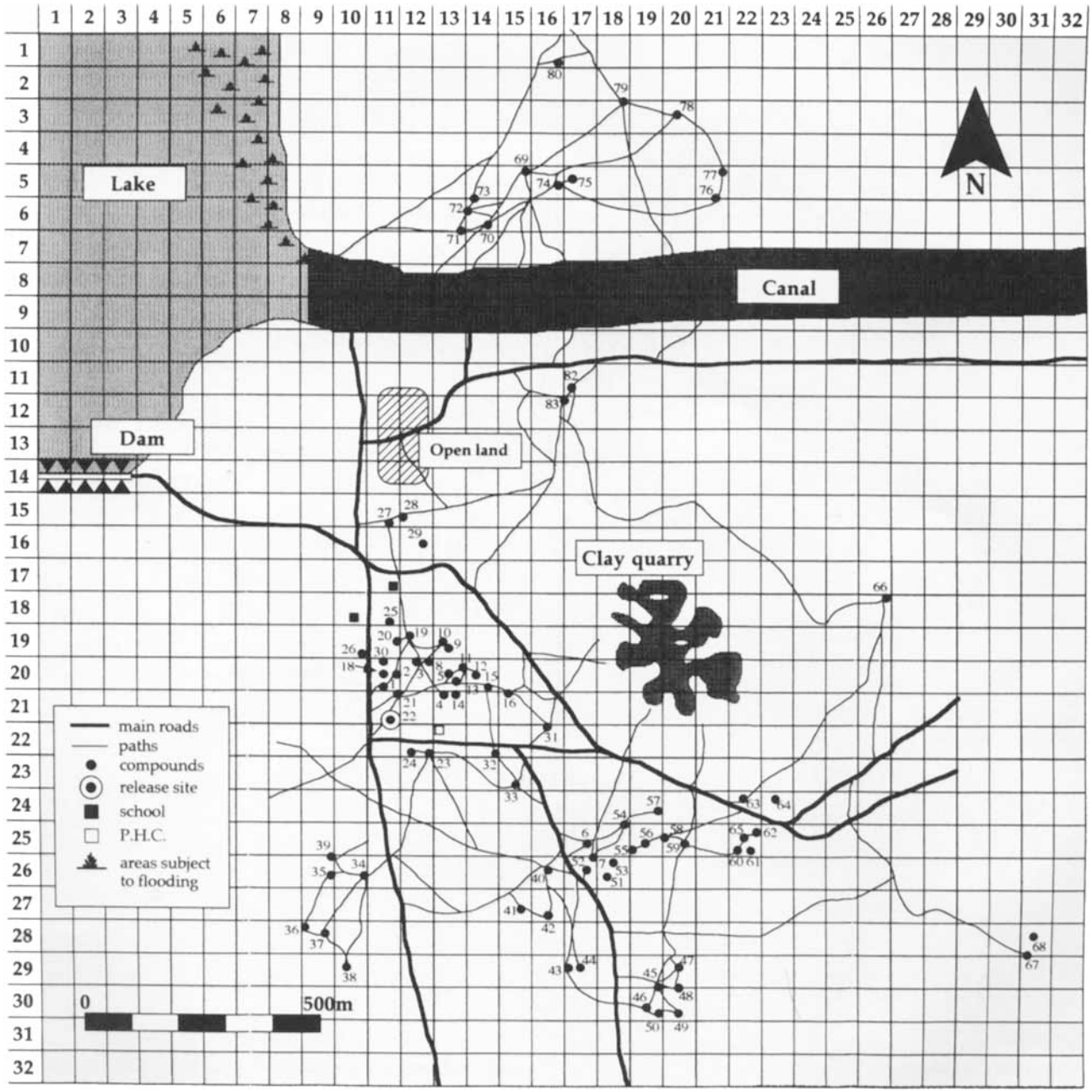


Fig. 2. Map of Goundri, showing the numbered compounds referred to in the text (dots on the map), and the release site.

showed that *An.gambiae s.l.* comprised ~95% of indoor-resting mosquitoes at Goundri.

The cages of marked mosquitoes for release were transported to an uninhabited hut in compound No. 22 (see map, Fig. 2). At *c.* 13.00 hours the sleeve of each cage was opened to allow the mosquitoes to escape. Most of the mosquitoes rested inside the cages and then left the hut around dusk. Mosquitoes that had died in the cage were counted, so that the numbers actually released could be determined.

In 1992, to reduce the handling of mosquitoes, the recapture step of the experiment was separated from the marking, thereby diminishing pre-release mortality from 16% in 1991 to 1% in 1992. For mark and release of all mosquitoes found resting indoors, male and female anophelines and culicines were collected directly into paper cups that had been dusted with fluorescent powder, then put into a storage cage and released as in 1991. Those simply captured for checking to determine if they had been marked previously were either aspirated into an undusted cup and killed, or collected by PSC, and subsequently examined under a stereo microscope with UV illumination.

From the many ways of using MRR data to estimate the density of adult mosquitoes (Blower *et al.*, 1981; Service, 1993), we

Table 1. Numbers of anopheline females (>95% *An.gambiae s.l.*) involved in mark–release–recapture experiments. Italicized numbers relate to the village of Goundri. IHC, indoor-resting collections; PSC, pyrethrum spray catches.

Date	Sampling action	Collection method	No. released	No. captured	No. recaptured
September 1991					
10	Release	IHC	1205	–	–
11	Release, recapture	IHC	1628	*1863*	*21*
12	Recapture nearby villages	PSC	–	2119	2
13	Release, recapture	IHC	1685	*2130*	*22*
14	Recapture nearby villages	PSC	–	2167	1
16	Release, recapture	IHC	1455	*1824*	*12*
17	Recapture nearby villages	PSC	–	721	0
18	Release, recapture	IHC	1287	*1671*	*16*
19	Recapture nearby villages	PSC	–	930	1
20	Recapture Goundri	IHC	–	*1283*	*24*
21	Recapture nearby villages	PSC	–	481	2
23	Recapture Goundri	PSC	–	*1201*	*11*
Total Goundri			7260	9972	106
Total all sites			7260	16390	112
September 1992					
5	Release	IHC	1607	–	–
7	Recapture Goundri	IHC	–	*2866*	*20*
8	Release	IHC	3580	–	–
9	Recapture Goundri	PSC	–	*2635*	*33*
11	Release	IHC	4150	–	–
12	Recapture Goundri	IHC	–	*3171*	*32*
14	Recapture Goundri	PSC	–	*1307*	*7*
15	Recapture nearby villages	PSC	–	854	3
16	Release	IHC	3315	–	–
17	Recapture nearby villages	PSC	–	884	2
18	Recapture Goundri	PSC	–	*2310*	*20*
21	Release	IHC	1202	–	–
23	Recapture Goundri	PSC	–	*490*	*3*
24	Recapture nearby villages	PSC	–	834	0
25	Recapture nearby villages	PSC	–	1152	3
28	Recapture Goundri	PSC	–	*439*	*1*
Total Goundri			13854	13218	116
Total all sites			13854	16942	124

limited our analysis to three methods: the Lincoln Index, the Fisher and Ford deterministic model, and Jolly's stochastic model. Details of these procedures are provided below with results of their application. Statistical methods employed for estimation of dispersal and survival are combined with the relevant sections of results.

Results

Recaptures

Goundri. The total number of anopheline females marked and released was 7260 in 1991 and 13,854 in 1992 (Table 1). The numbers of recaptures were 106 in 1991 and 116 in 1992, corresponding to recapture rates of 1.46% for 1991 (95% confidence limits 1.20–1.76%) and 0.84% (0.69–1.00%), respectively. These values are comparable to those obtained in previous MRR studies of *An.gambiae s.l.* (see Service, 1993). Fig. 3 shows the numbers of unmarked mosquitoes collected per hut (upper graphs), as well as the numbers recaptured 1–2 days (middle graphs) and 3–11 days (lower graphs) after release.

For the 1992 collections, nearly all the anophelines recaptured were identified to the species level. Only two *An.funestus* were found. Of the *An.gambiae s.l.* identified by PCR, *An.gambiae s.s.* accounted for 38.2% (95% c.l. 29.0–48.0%) and the remainder were *An.arabiensis*. In view of the species ratio difference between early and late September collections by spray catches, as reported in the study area description, we separated the marked recaptures into early (7–14 September) and late (18–28 September) collections. The relative numbers of *An.gambiae*:*An.arabiensis* were 34:54 in the early collections and 8:14 in the late collections, not significantly different ratios ($G = 0.039$; d.f. = 1; $P > 0.80$). The sibling species ratio among the marked recaptures, overall, differed slightly from the spray catches in that there was a moderate excess of *An.arabiensis* in the recaptured sample ($G = 3.805$; d.f. = 1; $P = 0.05$).

The numbers of *An.gambiae* and *An.arabiensis* recaptured within a 200-m radius from the release hut were 30:36. The numbers

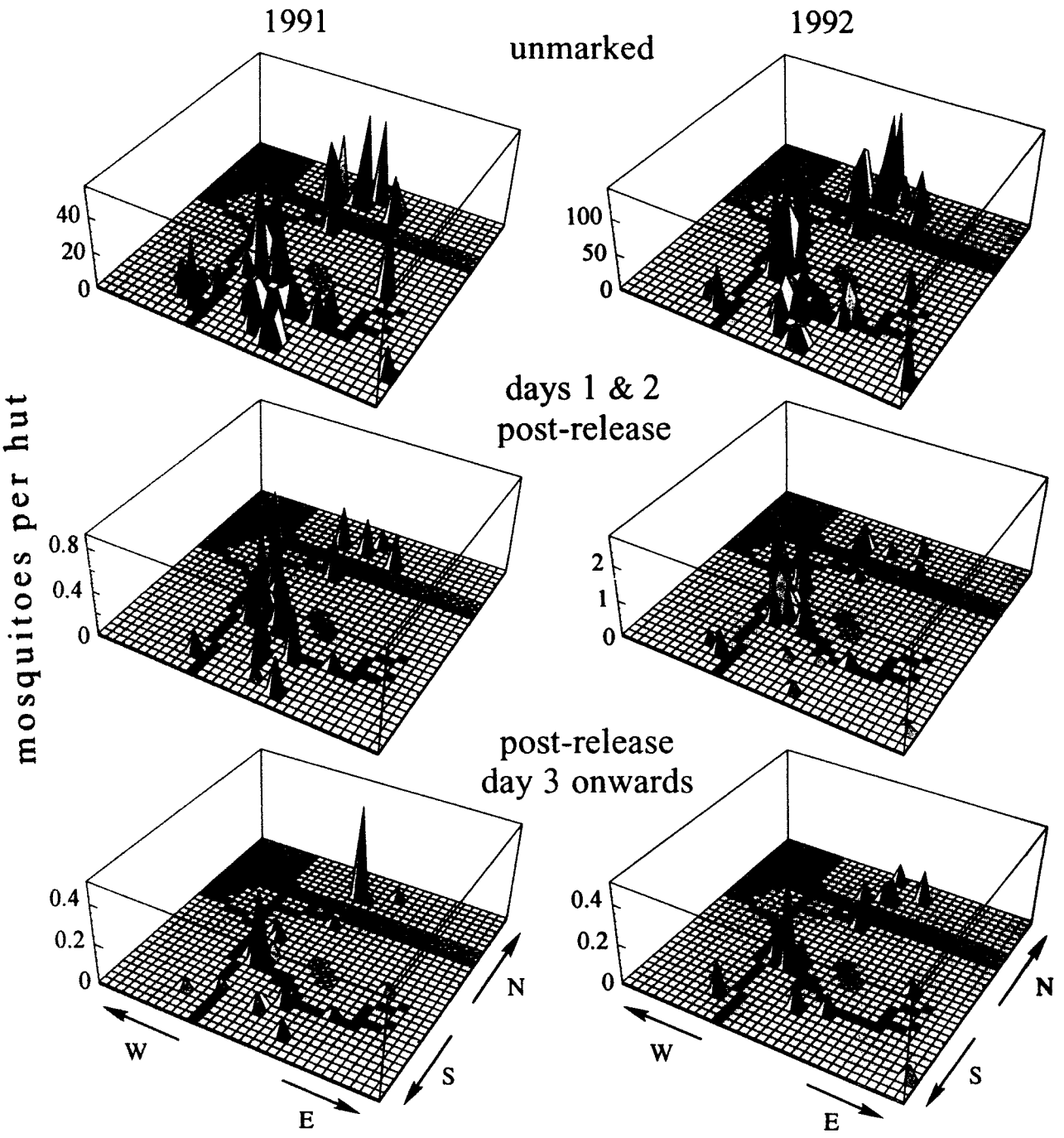


Fig. 3. Spatial distributions of *An.gambiae s.l.* (numbers per hut) at Goundri in 1991 and 1992: unmarked (top row) and marked mosquitoes recaptured 1 or 2 days post-release (middle row) or 3 or more days post-release (bottom row). The grid corresponds with Fig. 2. Roads and water areas are indicated by solid lines and hatch-marking, respectively.

recaptured beyond 200 m were 12:32 *gambiae:arabiensis*, showing a significantly higher proportion of the latter ($G = 3.775$; 1 d.f.; $P = 0.05$). Marked *An.arabiensis* females were recaptured more frequently in the southern sector of the village (compounds 34–68) as compared to the central sector (compounds 1–33) ($G = 3.246$, 1 d.f.; $P = 0.07$). Of the four marked males recaptured (Table 2), the single *An.arabiensis* had moved *c.* 950 m from the release site, whereas all three *An.gambiae s.s.* males were found less than 75 m from the hut where they were released.

Neighbouring villages. Table 3 gives the numbers of anopheline females collected and recaptured in villages around Goundri. All 14 recaptures came from three of the eight villages, 13 of them from two northern villages: Bagaren and Nangtenga. All 6 recaptures in 1991 and 8/9 recaptures in 1992 were *An.gambiae*

Table 2. Total number of males and culicines released and recaptured during the September 1992 mark–release–recapture experiment at Goundri. The vast majority of male specimens were *An.gambiae s.l.*, whereas culicines comprised mainly *Cx quinquefasciatus*. All marked recaptured males were *An.gambiae s.l.*

	Males			Culicines		
Village	Released	Captured	Marked recaptured	Released	Captured	Marked recaptured
Goundri	818	1605	4	219	595	0
Neighbouring villages	0	1097	0	0	336	0
Total	818	2702	4	219	931	0

Table 3. Numbers of anopheline females captured and recaptured in villages near Goundri.

Village	Total captured	Marked recaptured	Recapture rate (%)	No. of days after release
September 1991				
Bagaren	2398	4	0.17	1, 2, 3, 6
Managsombo	1134	0	0.00	–
Nangtenga	1107	2	0.18	8, 11
Sa	1453	0	0.00	–
Tanguen	326	0	0.00	–
Total	6418	6	0.09	–
September 1992				
Bagaren	740	2	0.27	7, 9
Kamsaoguen	141	0	0.00	–
Managsombo	48	0	0.00	–
Nangtenga	1572	5	0.32	4, 4, 4, 6, 14
Peul camp SW	126	0	0.00	–
Sa	364	0	0.00	–
Tanguen	332	0	0.00	–
Tanlarogo	401	1	0.25	9
Total	3724	8	0.21	–

s.l.; the remainder was 1 *An.funestus* from Nangtenga. Overall recapture rates were 0.093% in 1991 (95% c.l. 0.034–0.199%) and 0.215% (0.093–0.417%) in 1992.

The ratio of the recapture rate in nearby villages to that in Goundri provides an estimate of the mean proportion of the anopheline population in other villages which originated from Goundri (Rawlings *et al.*, 1981). That value was determined as 8.8% (95% c.l. 3.2–18.7%) for 1991 and 24.5% (10.6–47.5%) in 1992. Confidence limits were calculated by the method of Rawlings *et al.* (1981). From PSC surveys further afield we recaptured 1 marked *An.gambiae s.l.* in the village of Ramitenga, approximately 6 km north-west of Goundri, 16 days after its release.

Estimates of An.gambiae s.l. population size

Lincoln Index method. For this simple method of estimating population density (Blower *et al.*, 1981; Service, 1993), a mosquitoes are originally marked and released. It is assumed that the marked individuals then disperse at random within an enclosed area, mixing homogeneously with the unmarked ones. A total of n mosquitoes are then captured on a subsequent occasion, r of which are observed to be marked. The total population size, P, and its variance are then estimated to be :

$$P = \frac{an}{r} \text{ where } r \geq 20, \text{ or } P = \frac{a(n+1)}{r+1} \text{ where } r < 20,$$

$$\text{var } P = \frac{a^2 n(n-r)}{r^3}$$

From each series of recapture days, our calculations (Table 4) pertain only to the first recapture after release. For 1991 the estimated population density of *An.gambiae s.l.* ranged from less than 90,000 to nearly 384,000, with a median of *c.* 221,000. Estimates for 1992 were higher, ranging from about 230,000 to ∞, with a median of approximately 426,000. Because of the small numbers recaptured, the sampling errors of these estimates were high. The 1991 releases and recaptures were not independent and the 1992 data included a value of infinity. Therefore, as we cannot calculate overall confidence limits, we have taken median values for comparative purposes.

Fisher and Ford method. The method described by Fisher & Ford (1947), makes the same assumptions as the Lincoln Index

Table 4. Estimates of population size of endophilic female anophelines in Goundri, from mark–release–recapture experiments analysed by the Lincoln Index. Recaptured numbers refer to the first recapture after release. Median values are shown in italics. The standard error is calculated as the square root of the variance. Confidence limits have been calculated from the binomial variance of the recapture ratio *n/r*. If females comprise half the total adults, then the estimated total population size should be twice these figures.

Release date	No. released (*a*)	Total captured (*n*)	Marked recaptured (*r*)	Population size (*P*)	Standard error	95% Confidence limits	
September 1991							
10	1205	1863	21	106,901	23,196	75,003	186,008
11	1628	2130	13	247,805	73,755	172,990	582,335
13	1685	1824	7	384,391	165,631	252,424	1,684,734
16	1455	1671	10	*221,160*	76,654	150,271	636,382
18	1287	1283	18	86,974	21,470	62,887	169,478
September 1992							
5	1607	2866	20	230,283	51,313	160,282	408,838
8	3580	2635	26	362,819	70,803	262,440	587,549
11	4150	3171	27	487,394	93,399	354,316	780,572
16	3315	2310	17	*425,609*	108,847	305,676	855,746
21	1202	1283	0	∞	–	–	–

about population containment and mixing. By also assuming a constant mortality rate, information may be incorporated from recaptures on all days post-release, suitably adjusted for the estimated mortality. MRR data were summed on trellis diagrams (Fig. 4) covering all the dates sampled.

The Fisher–Ford procedure estimates the mortality rate by comparing the fit of an observed vector to a derived vector: the best-fitting derived column is assumed to give the survival rate (Service, 1993). We used two ways to measure the fit: mean absolute difference, and mean squared difference between the two vectors, giving similar estimated survival rates (Table 5).

For 1991 the lower estimates of *An.gambiae s.l.* population size were well below 100,000, whereas the highest estimate was over 205,000, with 134,000 as the mean of medians. Corresponding estimates for 1992 were higher, ranging from *c.* 74,000 to nearly 570,000, with a median of *c.* 326,000 (Table 5). These values were somewhat lower than the Lincoln Index annual estimates (221,000 and 426,000) given in Table 4.

Jolly's method. In theory, the probabilistic model proposed by Jolly (1965) uses the information from multiple recaptures in the most efficient way (Service, 1993). The principle of the method is to estimate the total number of marked mosquitoes present in the population, *M(i)*, from those originally released, *s(i)*, on each sampling occasion, *i*, and to divide it by the proportion of marked mosquitoes in the population $\alpha(i)$, as estimated from the ratio of the total number of recaptures on each day irrespective of mark type *m(i)*, over the total number caught *n(i)*. Loss of marked mosquitoes is taken into account in the estimation of *M(i)* from parameters *R(i)* and *Z(i)*, which are, respectively, the total number of recaptures for each cohort of marked *s(i)* on each release day, and the total number of recaptures marked previous to day *i*, not caught on day *i* but subsequently. As stated in Macdonald *et al.* (1968), Jolly advised use of the corrected formula

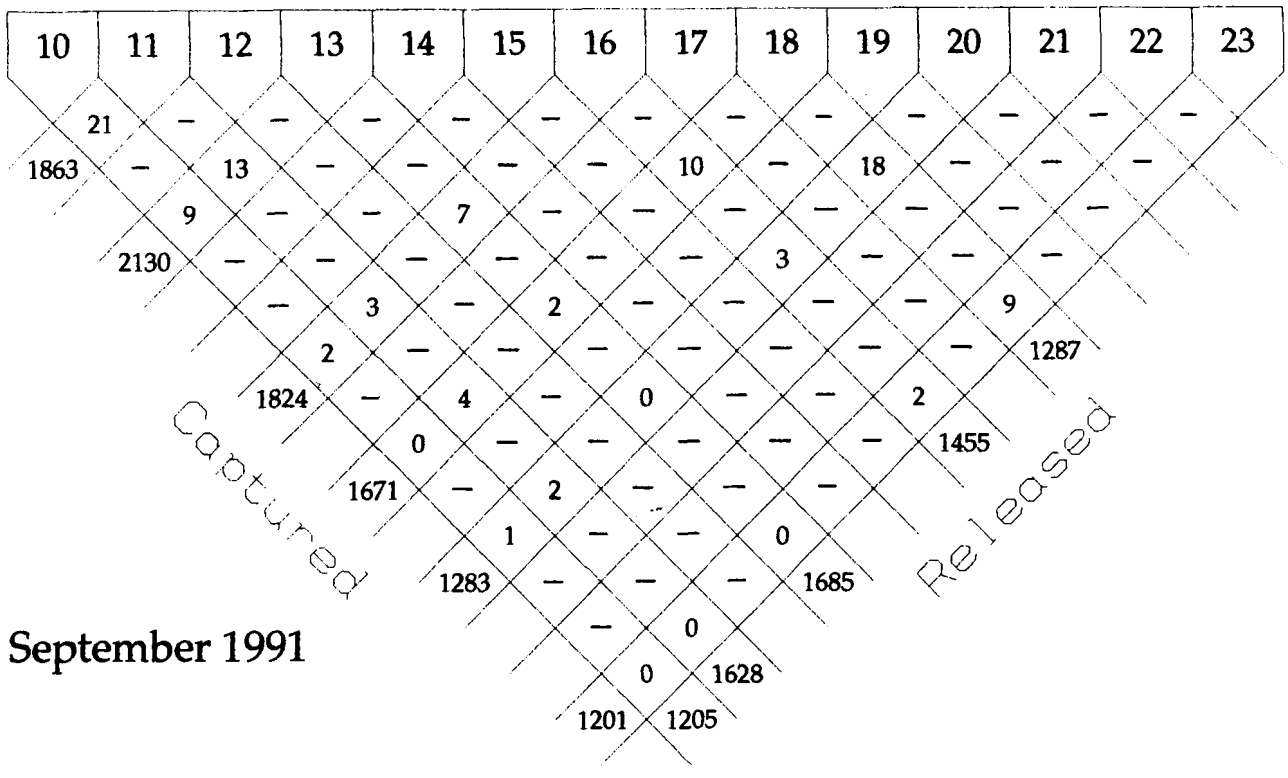
$$M_i = \frac{s_i(Z_i + 1)}{R_i + 1} + m_i$$

to compensate for overestimation of *M(i)* when the number of recaptures is low. Apart from estimating the total population size *N(i)*, it is possible to calculate the probability that an individual will still be alive in the population in the time interval $(i, i + 1)$, $\Phi(i)$, and the number of mosquitoes entering the population and still alive during the same period $(i, i + 1)$, $\beta(i)$.

For 1992, population estimates were highly variable between different dates and not consistent with the estimates obtained with the other two methods, whereas for 1991 the figures are more homogenous, but standard errors are still high (Table 6). The median values for *An.gambiae s.l.* population size are approximately 130,000 for 1991 and 163,000 for 1992, similar to the other estimates (Tables 4 and 5).

PSC method. Carefully performed pyrethrum spray catches should obtain most of the mosquitoes inside a closed dwelling. A crude estimate of the total endophilic fraction of the population can be obtained when the geometric mean number of mosquitoes sampled per hut is multiplied by the total number of huts present in the village, provided that displacement of endophilic mosquitoes during sampling does not introduce bias (Elliott, 1977). It was difficult to cover all holes and crevices, especially in huts made of mud-bricks with open eaves all around, to prevent mosquitoes from escaping. Moreover, mosquitoes may hide deep in the thatched roof before dying, preventing them from falling down on the collecting sheets. Gillies (1955) estimated the efficiency of spray catches to be in the range of 80–90%. We assumed a value of 80% for *An.gambiae s.l.* in our study. The 1992 population size estimates obtained in this way, median value 7056 (Table 7), were much lower than those obtained by other methods (cf. median values of *c.* 130,000–426,000 in Tables 4–6).

Among the reasons that PSC estimates are lower than other estimates may be interchange between the endophilic and exophilic fractions of the population. The proportion of the population resting outdoors is unknown, so it is difficult to interpret these discrepancies. The extent to which these figures differ suggests that either the mathematical models greatly



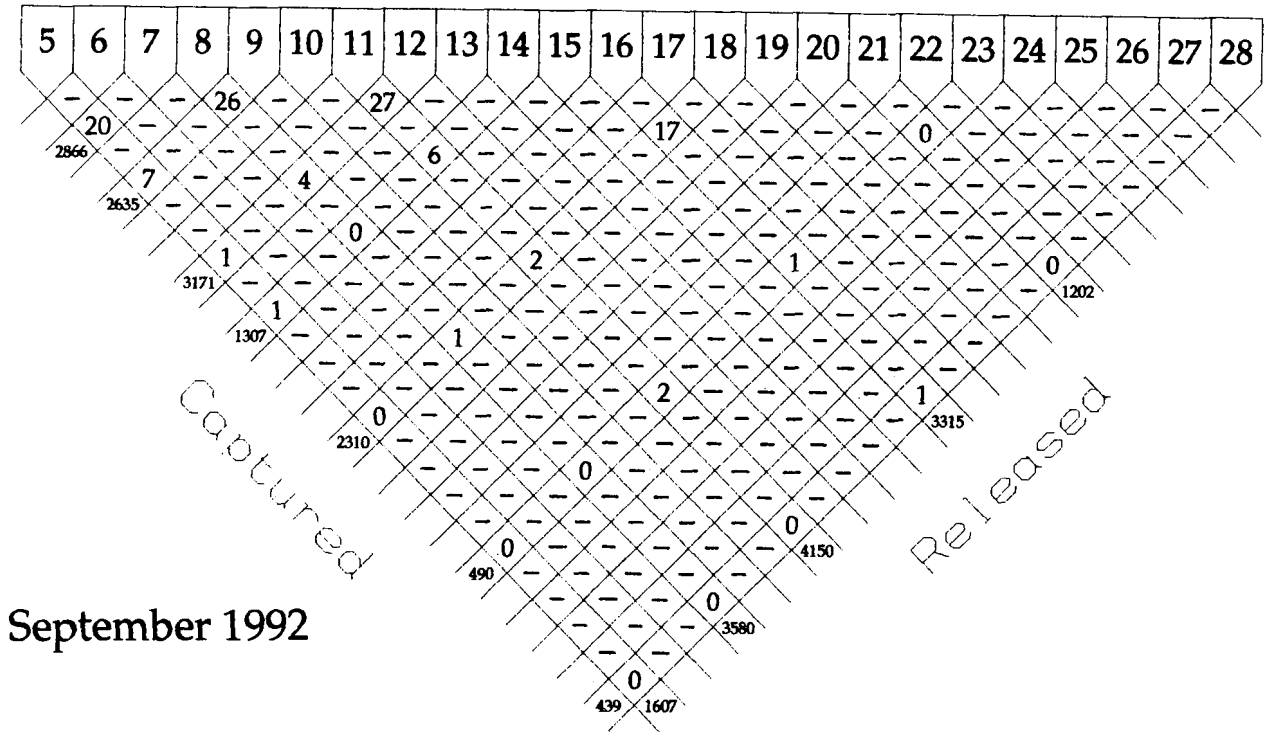


Fig. 4. Trellis diagrams of released, captured and recaptured female anophelines for calculation of Fisher and Ford population size estimates. Sampling dates are given along the top row. Columns descending diagonally towards the right show the numbers of those released on that day that were captured on the date corresponding to the right-ascending column intersecting with it. Totals released on each date are shown on the right edge. Totals captured on each date are shown on the left edge. Entries in squares formed by intersecting columns show the number of mosquitoes recaptured for that combination of release and recapture dates (– indicates no recapture attempt). For example, in 1991, the '21' entered in the first cell on the upper left of the trellis indicates 21 mosquitoes were captured on 11 September that had been released on 10 September. The marginal totals show that the number released on 10 September was 1205, and the total number captured on 11 September was 1863.

Table 5. Estimates of population size of endophilic female anophelines in Goundri from mark–release–recapture experiments (Fig. 4) analysed by the method of Fisher & Ford (1947). Median values are shown in italics. If females comprise half the total adults, then the estimated total population size should be twice these figures.

Recapture date	Population size	
	Mean absolute fit	Mean square fit
September 1991		
11	106,901	106,901
–	*135,363*	*132,675*
13	163,825	158,448
16	205,351	190,808
18	171,505	161,154
20	88,984	83,395
23	59,314	51,572
Estimated daily survival rate	0.689	0.672
September 1992		
7	166,679	155,441
9	*334,514*	325,321
12	568,655	535,405
14	561,329	459,644
18	372,431	*317,471*
23	246,725	195,430
28	131,734	73,604
Estimated daily survival rate	0.724	0.675

overestimate the real population size, and/or the exophilic fraction represents a relatively high proportion (unsampled with PSCs) of the whole population. In any case, the definition of mosquito population size is subjective, since there are no boundaries to the movement of such mobile insects from village to village.

For any method of estimating population size to be accurate, sampling should not be biased. For example, collection sites should be equally attractive to mosquitoes of all ages. This can be tested by the distribution of unmarked mosquitoes: is it random or not? We tested the PSC data (Table 7) for agreement to a Poisson distribution, using a χ^2 test for departure of the variance: mean ratio from unity (Elliott, 1977). Agreement to a negative binomial distribution was tested using U (to test for a difference between the sample estimate of variance and the variance in a negative binomial) and T (to test for a difference between the sample estimate of the third moment and the expected third moment) statistics, according to the guidelines given by Elliott (1977). In all instances the difference was highly significant, as shown by very high values of the variance:mean ratio, sometimes exceeding 100 (Table 7), demonstrating that *An.gambiae s.l.* were non-randomly distributed among our PSC collection sites (Figs 2 and 3).

Dispersal

Estimates of density and dispersal from MRR experiments typically assume that (a) the populations are spatially limited, (b) the entire population of released mosquitoes can be sampled, and (c) sampling from all locations is equally effective. In our study, however, none of these assumptions was fully met. The difficulties are compounded when huts are arranged in irregular patterns, so the traditional methods of measuring dispersal cannot be applied, as discussed by, for example, Wright (1978) and Service (1993, p. 724). A more robust method for analysis is required.

Spatial distributions of unmarked *Anopheles* and marked recaptures (numbers per hut) are portrayed in Fig. 3. Dispersal was estimated by fitting two simple models of mosquito movement to the observed data, then finding those parameters of the model that minimized the difference between the

Table 6. Population size estimates of endophilic female anophelines in Goundri, from mark–release–recapture data analysed by Jolly's stochastic model. See text p. 000 for description of methods and symbols.

i	$n(i)$	$s(i)$	$R(i)$	$Z(i)$	$m(i)$	$M(i)$	$\alpha(i)$	$N(i)$	$\Phi(i)$	$\beta(i)$	SE[$N(i)$]	SE[$\Phi(i)$]
September 1991												
1	1205	1205	33	–	–	–	–	–	–	–	–	–
2	1863	1628	22	12	21	941	0.011	83,946	0.868	141,918	33,888	0.0067
3	2130	1685	9	12	22	2213	0.010	214,210	0.238	89,228	104,107	0.0068
4	1824	1455	15	9	12	921	0.007	140,049	0.497	53,267	69,858	0.0103
5	1671	1287	9	8	16	1174	0.010	122,641	–	–	65,780	–
6	1283	0	–	9	24	–	0.019	–	–	–	–	–
7	1201	0	–	–	11	–	–	–	–	–	–	–
September 1992												
1	1631	1607	29	–	–	–	–	–	–	–	–	–
2	2866	3580	31	9	20	1139	0.007	163,183	0.146	30,949	68,927	0.0052
3	2635	4150	37	5	33	688	0.013	54,957	–	–	24,976	–
4	3171	0	–	10	32	–	0.010	–	–	–	–	–
5	1307	3315	19	–	7	–	0.005	–	–	–	–	–
6	2310	1202	0	2	20	3626	0.009	418,803	–	–	–	–
7	490	0	–	0	3	–	0.006	–	–	–	–	–
8	439	0	–	–	1	–	0.002	–	–	–	–	–

Table 7. Williams' geometric mean number of *An.gambiae s.l.* collected in Goundri by means of pyrethrum spray catches in September 1992. The distribution of individuals between huts does not conform either to a Poisson ($P < 0.001$), or to a negative binomial distribution ($P < 0.001$) on all sampling dates. The estimated endophilic population size is given for each sampling occasion, assuming an 80% efficiency of the spray catch. The variance:mean ratio refers to the original, untransformed counts.

Date	No. of huts sampled	Geometric mean	95% Confidence limits		Variance: mean ratio	Estimated endophilic population size	95% Confidence limits	
9	36	44.5	31.3	63.5	117	23,552	16,531	33,555
14	35	13.3	7.8	23.0	76	7,056	4,099	12,148
18	33	45.6	33.2	62.6	61	24,091	17,530	33,108
23	27	9.3	5.8	14.7	25	4,893	3,072	7,793
28	25	10.6	6.6	17.1	20	5,596	3,470	9,024

simulated and observed values. It was necessary to pool data extensively so that we could make statistical measurements of how well the simulations fit the data. This was done in two ways, by distance and by day after release. Pooling by date: in 1991 we analysed the data for 1–5 days after release separately, but pooled the mosquitoes recaptured on days 6–7 and on days 8–10; in 1992 we pooled days 6–7 and days 9–12. We recognized one, three or five distance groups, in annuli demarcated by 200 and 500 m, or demarcated by 100, 180, 480 and 640 m from the release site. This pooling was required in order to have a minimum number of marked mosquitoes in each day and distance class. In 1991, to avoid heterogeneities, recaptures caught by means of spray catches were excluded from the analysis. In 1992, because it was difficult to distinguish between *An.funestus* and *An.gambiae s.l.* at time of release, we lumped all species together for this part of the study, though few (<2%) were *An.funestus*. Numbers of recaptured mosquitoes in each category are shown in Table 8.

Each released mosquito was assigned to one processor on a CM2 Connection Machine, with variables describing location and relevant dispersal parameters stored in the processor memory. Because of the small number of recaptures each day, the different releases were pooled: 7260 processors were used for the 1991 simulations and 13,854 for those released in 1992. Two models of dispersal were used. The program for movement was stepped for all processors in parallel, and the collective behaviour monitored. At fixed intervals the simulated mosquitoes were then associated with nearby huts, at positions corresponding to those of Goundri in Fig. 2. The goodness of fit between simulation and observation was measured by the squared difference between simulated and observed numbers of mosquitoes, pooled over distances for Model I and over compounds for Model II. This method fully exploits the parallelism of the CM2, and so could be done quickly. We also performed serial versions of this process, coded independently, on Sun and NeXT workstations to help insure against programming error. As the results were comparable, here we do not distinguish among them.

The space of dispersal parameters was searched using Powell's method, a variant of conjugate gradient search (see Press *et al.*, 1992). In all but a few instances the process converged; when it did not, the search was stopped arbitrarily at a depth of 200 and the best value taken. Because the movement algorithm required random numbers and changed variables to search in a pre-assigned order, the fit depended somewhat on the random seed, the starting place, and the order in which the variables were searched. To ameliorate this problem, we began the search with thirty-three different random seeds, each with a different starting location and order of variables, following an independent search for the optimum along a path determined by that combination of seed and starting conditions. Even when those optima had been reached, random numbers for movement could give somewhat different results. We therefore took the average of twenty-four simulations from each optimum to represent the fit.

Model I. The first model for dispersal assumed that all female mosquitoes were released at the same location, shown in Fig. 2, and performed the following sequence of steps:

(1) The mosquito decides whether to move or not to move, according to a random number drawn from the interval [0, 1] and compared to the parameter NON_MOVE_RATE. If the random number is greater than NON_MOVE_RATE it is assumed to move, and otherwise not to move.

(2) If the mosquito is to move, then: (a) it picks a direction at random from the interval [0, 360); (b) it chooses a distance to move, from the interval [0, MAX_MOSQUITO_SPEED]; (c) it changes its location according to the forgoing.

(3) The mosquito may or may not survive. For each day after the first we assume that the probability of survival is governed by MORTALITY, from the interval [0, 1].

All probabilities were drawn from a uniform distribution. This was repeated for seventy-two time-steps per day, at the end of which time mosquitoes were associated with huts to assess the fit to observation. This was done by calculating the density of mosquitoes (per m^2) around each hut, and multiplying that number times the area from which the hut attracted, HUT_AREA. All mosquitoes in an area of HUT_AREA surrounding a hut were assumed to be attracted to it.

Model II. It is apparent that real dispersal of mosquitoes is more complicated than described by Model I. For example, gonotrophic state influences movement, and a higher concentration of huts is more likely to attract mosquitoes from the outside (Brengues & Coz, 1973; Gillies, 1988). We attempted to incorporate some of this complexity in a second model, though some of the rules were necessarily complex and arbitrary. As with the first model, we assumed that all female mosquitoes were released at the same location, shown in Fig. 2, and performed the

Table 8. Fit between observed data and computer simulations of dispersal around Goundri, showing the best fit for two models of dispersal. These models and the relevant parameters are described in the text, p. 213.

Day after release	Distance (m)	Observed	Model I		Model II	
			Simulated	Fit	Simulated	Fit
September 1991						
1	0–200	6	13.0	49.0	9.9	15.2
	201–500	4	4.7	0.5	2.4	2.6
	>500	11	7.7	10.9	5.4	31.4
2	0–100	10	5.9	16.8	3.4	43.6
	101–180	7	8.9	3.6	4.9	4.4
	181–480	13	10.9	4.4	6.3	44.9
	481–640	5	4.5	0.3	2.4	6.8
	>640	6	8.2	4.8	5.3	0.5
3	0–200	11	5.7	28.1	5.6	29.2
	201–500	2	4.2	4.8	4.4	5.8
	>500	3	5.2	4.8	5.2	4.8
4	Whole village	3	4.9	3.6	2.7	0.1
5	Whole village	5	7.5	6.3	4.4	0.4
6-7	Whole village	6	5.7	0.1	5.0	1.0
8–10	Whole village	3	2.4	0.4	2.1	0.8
Total		95	99.4	138.4	69.4	191.3
September 1992						
1	0–100	23	11.8	125.4	10.6	153.8
	101–180	14	21.3	53.3	17.9	15.2
	181–480	8	12.9	24.0	11.1	9.6
	481–640	4	3.0	1.0	3.3	0.5
	>640	6	0.9	26.0	1.4	21.2
2	0–100	12	5.2	46.2	2.4	92.2
	101–180	10	7.3	7.3	3.8	38.4
	181–480	4	3.8	0.0	3.4	0.4
	481–640	1	2.4	2.0	1.4	0.2
	>640	10	1.1	79.2	1.3	75.7
3	Whole village	6	8.1	4.4	6.4	0.2
4	Whole village	11	11.7	0.5	10.6	0.2
6–7	Whole village	4	6.9	8.4	6.4	5.8
9–12	Whole village	5	1.3	13.7	1.5	12.3
Total		118	97.7	391.5	81.5	425.4

following steps (for each time step, assuming 2 days mean duration of the gonotrophic cycle).

(1) The mosquito decides whether to move or not to move, depending on its feeding state. If the gut is entirely empty, it is assumed to have just laid and needs to feed. If the mosquito has already blood-fed, then it needs to rest. In either event the mosquito will tend to stay in its current hut, otherwise it will remain only with a probability proportional to its feeding state.

(2) If the mosquito has almost digested its bloodmeal it is assumed to be ready to oviposit, forage again and obtain another bloodmeal. It will otherwise digest its bloodmeal by a fixed amount, chosen to make the gonotrophic cycle last 2 days.

(3) If the mosquito is to move, then: (a) it picks a direction at random from the interval [0, 360); (b) it chooses a distance to move at random, from the interval [0, MAX_MOSQUITO_SPEED]; (c) its location changes accordingly.

(4) The mosquito may or may not enter a hut, depending on a probability calculated as a function of distance and concentration of huts in the area. Mosquitoes are assumed to enter a hut in the compound if they are within a distance HUT_ATTRACT* (number of huts in the compound).

(5) The mosquito may or may not survive. For each day after the first we assume that the probability of survival is governed by MORTALITY, from the interval [0, 1].

Again all probabilities were drawn from a uniform distribution and there were seventy-two time steps per day. For Model I the spatial units were metres; for Model II they were in grid units from our map, approximately 60 m. Best-fitting values of the parameters are shown in Table 9.

It is apparent from Table 8 that the first, simpler model fits the recapture data for both years better than does the more detailed Model II. For 1991 the mean square difference for Model I is 138.4 and for Model II it is 191.3. For 1992 the mean square difference for Model I is 391.5 and for Model II it is 425.4. This might result from assumptions in the second model that were

Table 9. Best-fitting parameters of two theoretical models of simulated mosquito dispersal around Goundri, against September 1991/92 mark–release–recapture field data. For an explanation of the parameters, see text pp. 213–214.

Parameters	1991	1992
Model I		
Non_Move_Rate (per time step)	0.086	0.125
Max_Mosquito_Speed (m/time step)	153.0	85.6
Mortality (per day)	0.183	0.103
Hut_Area (m^2)	685.0	182.0
Mean distance moved (m/day)	636	348
Model II		
Max_Speed (cells/time step)	2.43	1.85
Mortality (per day)	0.172	0.052
Hut_Attract (half cells for drawing area)	0.0180	0.0122
Translated into Model I terms:		
Non_Move_Rate (per time step)	0.158	0.131
Max_Mosquito_Speed (m/time step)	145.8	110.7
Mortality (per day)	0.172	0.052
Hut_Area (m^2)	67.1	31.0
Mean distance moved (m/day)	571	443

wrong, for which no amount of parameter adjustment could compensate. Alternatively, for Model I there were four parameters that could be modified to fit the data, whereas in Model II there were only three free parameters. Both models made assumptions that were simplified, and it might have been that the simplifications of Model I in some way cancelled better than those of Model II. Whatever underlies the remaining differences between simulation and observation, both models were apparently crude and inexact.

We made no attempt to search through the space of all models to locate which is best; that would have been too formidable a task. Moreover, as we could not distinguish between sibling species, chromosomal forms or ovarian conditions of live mosquitoes, such an attempt could not validated. The point emerges clearly, however, that dispersal in 1991 was different from that in 1992, and in both cases was very great, exceeding several kilometres over a mosquito's life-span.

Survival

The Fisher–Ford, Jolly, and simulation analyses described above all provided estimates of daily survival. We also examined other ways to estimate survival. An especially simple model for MRR data assumes that the loss of marked recaptures is described by the function.

$$A = Nap^n$$

where A = number of marked females, N = total numbers marked and released, a = recapture rate, p = survival rate, and n = days after release (Service, 1993). Plotting the logarithm of the number of recaptures (log A) over days after release (n) it is possible to estimate p as the antilogarithm of the slope of the fitted regression line. The underlying assumption of this model is that both the recapture rate and the daily probability of survival must be constant. Fig. 5 shows the regression lines fitted to the 1991 and 1992 data. The 1991 scatter plot refers to a mixture of anopheline species, the 1992 scatter plot refers to *An.gambiae s.l.* only. Both regression slopes are significantly different from zero ($P < 0.001$) and have high coefficients of determination (1991: $r^2 = 0.791$; 1992: $r^2 = 0.774$). The regression equations are $y = 1.290 - 0.133n$ for 1991 and $y = 1.327 - 0.129n$ for 1992. The estimated probability of survival is 0.736 (95% c.l. 0.664–0.818) for 1991 and 0.743 (0.672 – 0.822) for 1992. Points on the far right side of the abscissa for the 1992 scattergram suggest the relationship is not completely linear. Apparently those individuals surviving over 9 days after release show a higher probability of survival than expected with a constant p.

We also estimated daily survival from the formula for the proportion of mosquitoes with sporozoites in their salivary glands found in the deterministic malaria model of Macdonald (1957):

$$s\frac{p^n ax}{ax - \log_e p}$$

where s = the sporozoite index, p = the daily survival probability of the mosquito population, n = time taken for completion of the extrinsic cycle, a = the average number of people bitten by one mosquito in one day, and x = the proportion of people showing

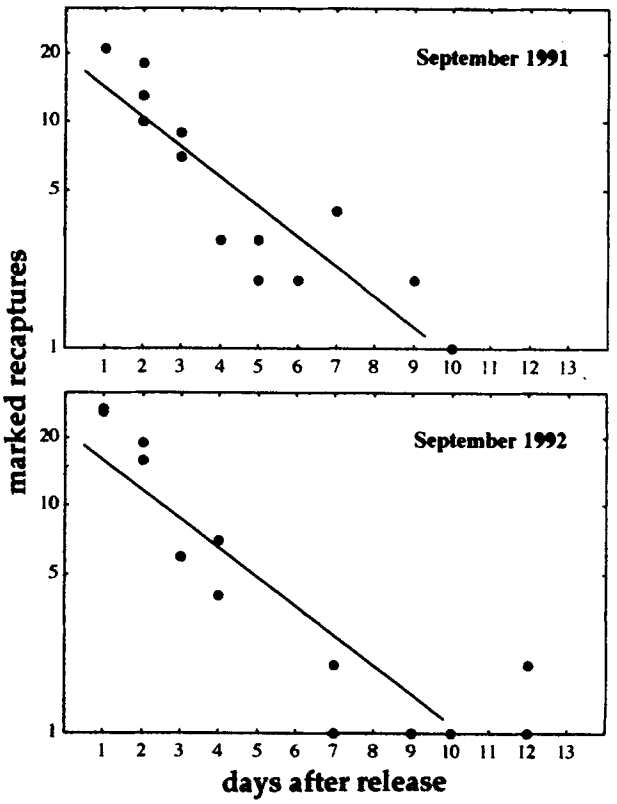


Fig. 5. Regression of the logarithm number of marked recaptures over the days after release; the 1991 data (upper half) refer to all anopheline females, the 1992 data (lower half) to *An.gambiae s.l.* females only. The antilogarithm of the slope of the regression line gives an estimate of the daily survival probability (assumed constant). For further explanations, see text p. 215.

Table 10. Summary of daily survival probabilities obtained with different techniques. Fisher and Ford (a) and (b) estimates refer to the mean absolute and square fit, respectively. Jolly's estimate for 1991 is the median of several dates (see Table 7). Numbers in parentheses are 95% confidence limits for the 'decay' model, and estimated theoretical limits for the Macdonald model (the latter not referring to a particular year – it is a mean figure instead; see text for details).

Estimation method	1991	1992
Fisher and Ford (a)	0.689	0.724
(b)	0.672	0.675
Jolly	0.705	0.383
Recaptures 'decay'	0.736 (0.664–0.818)	0.743 (0.672–0.822)
Simulation Model I	0.817	0.897
Simulation Model II	0.828	0.948
Macdonald model	0.824 (0.731–0.885)	

parasitaemia. Using field data collected in Goundri during September 1990 and 1991 (Merzagora, 1993) we estimated s, a and x, and calculated p by iteration. Putting constraints on the first three parameters it was also possible to calculate the estimated theoretical limits inside which p should lie. The values we used for the most probable situation are $s = 0.10$, $n = 10$, $a = 0.48$ and $x = 0.90$, whereas the empirical constraints are $s = 0.05 - 0.15$, $n = 8 - 12$, $a = 0.283 - 0.5$, $x = 0.80 - 0.95$. The distribution of such estimates was skewed towards values higher than the most likely p.

The results from all such calculations of daily survival are assembled in Table 10. If we take the Macdonald estimate to give the most reliable values, then figures from the analytical study of MRR data tend to overestimate mortality, probably because of the high loss of marked individuals from the recapture area. Simulation estimates for 1991 are well within the expected theoretical limits, whereas those for 1992 are close to the upper theoretical limits.

Discussion

Dispersal

The principal paradigm for measuring dispersal in insects has been mark–release–recapture experiments, in the manner analysed by Dobzhansky & Wright (1943) for *Drosophila pseudoobscura* Frolova. As such experiments are performed today, traps are usually placed in a cross-shaped pattern. Then flies are collected, taken to the centre of the cross, marked and released. If (a) dispersal is uniform and (b) the traps are arranged in a sufficiently regular pattern, then the distribution should result in a three-dimensional bell-shaped curve which flattens as time goes by. Wright showed how to adjust mathematically for the flies caught at various distances so that the distribution could be 'filled in', giving the statistical illusion that flies are sampled from throughout the area, and a single measure of dispersal could then be estimated and its sampling distribution calculated. Many researchers have subsequently used these techniques, or suitable variants, to obtain more refined measures of dispersal by *D.pseudoobscura* and its relatives (see Taylor & Powell, 1983).

It should be emphasized that Wright's method of calculation absolutely requires that dispersal is uniform and the traps are arranged in a regular pattern. In very few instances, however, are Wright's assumptions likely to be realized. Adjustments are possible in a few special cases: in particular, weighted averaging facilitates the proper adjustment (e.g. Linthicum *et al.*, 1985) when sampling points are not in a regular pattern but it can be assumed that dispersal is uniform. In general, however, we must expect that individuals will move at different rates in different areas – sometimes with direction, sometimes randomly – and collections can be made from only a few special locations which are distributed quite irregularly. In such cases Wright's method will not work, and a more general method must be used.

One step in that direction was suggested by Dobzhansky *et al.* (1979). They measured dispersal of *D.pseudoobscura* over a heterogenous area, with unequal dispersal rates in the various microhabitats. Here we have repeated their approach, using *An.gambiae s.l.* as an experimental organism, and attempted to fit two structurally different models of dispersal to the data. One of these models (Model I) assumed more or less random movement, whereas the other (Model II) allowed for limited directional movement and for gonotrophic cycling. Based on conformance to knowledge about other aspects of this species' ecology, most notably survival, it appears that both models gave better estimates of dispersal and of survivorship than had otherwise been available, but truly independent validation has been possible for survivorship alone.

In the past, several approaches to the problem of describing and measuring mosquito dispersal have led to the formulation of regression equations relating the drop in densities to the distance from the release point. Service (1993) pointed out that these equations have only empirical value and, lacking a general sound theoretical model to justify their formulation, the regression parameters are difficult to interpret in any useful biological way, a point also discussed by Rudd & Gandour (1985). Of course, the questions to be asked in such an analysis may also be specific and appropriate for that analysis. For example, one may be interested only in the extreme flight range of the population when applying control measures in single villages. In such instances the empirical approach might still be useful. But when mean

dispersal or detailed mechanisms governing the process of dispersal are the main interest, then the approach used here is preferable, because it leads to the understanding of the general process.

Models I and II are oversimplified, and include many rough guesses and estimates. We are currently engaged in attempts to detail species differences and the role of gonotrophic state. In spite of this, it does appear that the model parameters are within the range of independent knowledge about the biology of these species. For example, the maximum speed of dispersal in this study was found to be around 15–25 cm s^{-1}; this is well below the physiological capabilities of mosquitoes, which can fly at speeds up to 2.5 m s^{-1} on a flight mill (Clements, 1963) and probably around 50–80 cm s^{-1} when approaching a host in an odour plume (Gillies & Wilkes, 1981; Costantini *et al.*, 1993). The radius of 'attraction' of a hut has been estimated to be around 5–15 m; this is well within the range of attraction of a carbon dioxide plume generated by a flow of about 300 ml min^{-1}, according to Gillies (1980). Daily mortalities were fitted to be around 0.10–0.20, well within the range of what has been estimated for *An.gambiae s.l.* in other field studies: 0.16 by Gillies (1961) and 0.15–0.21 by Gillies & Wilkes (1965). It must be stressed, however, that the daily survival probability of *An.gambiae, An.arabiensis* and *An.funestus* is probably not constant, but increases with age (Clements & Paterson, 1981).

We note that recapture data from the neighbouring villages suggests a somewhat greater degree of movement than that estimated from the fit to the data for Goundri alone. Further, the mean distance moved per day estimated by the computer simulations is somewhat lower than that found by Gillies (1961) in Tanzania. This might be a result of differences between East African and West African populations, a result of environmental differences, or both. The possibility that laboratory-reared mosquitoes disperse more than wild-caught adults, as found for *An.culicifacies* by Rawlings *et al.* (1981), must also be kept in mind. Though far from conclusive, our results suggest possible differences in dispersal between *An.gambiae* and *An.arabiensis*. For example, concentration of cow herds in the southern part of the study area might have attracted more *An.arabiensis*, as this species tends to be the more zoophilic (White, 1974). The relatively high mobility of the *An.gambiae* complex in rural areas has been demonstrated elsewhere (Gillies, 1961; Quiñones, 1991; Robert & Carnevale, 1991; Thomson *et al.*, 1995), whereas in urban situations these species seem to disperse to a lower degree (Sabatinelli *et al.*, 1986; Manga *et al.*, 1993). This is probably because hosts and breeding sites are more concentrated in towns. In view of the high malaria sporozoite rates, frequently around 10% (Merzagora, 1993), recorded in the local vector population, the mosquito dispersal rates indicated by the present study would promote panmixia of *Plasmodium falciparum* in the same area, even without human population movement.

We did not try to detect dispersal of *Anopheles* other than random or weak directional movement associated with clustering. Several factors which might have influenced the direction of movement are confounded. Wind blowing northeastwards could have played a role. The heterogenous distribution of breeding sites in the area seems likely to be more important, as indicated by the concentration of some distant-fliers (caught in the huts near the lake) recaptured within the village of Goundri. In this case, breeding sites might act also as a 'corridor' to facilitate dispersal towards the northern villages nearby.

Density

The analysis of population absolute densities by the Lincoln Index assumes that there is no gain (due to immigration and/or emergence of new adults) or loss (due to emigration and/or mortality) at the same time. In view of the estimated mortality and long-range dispersal, that assumption is clearly violated. It may be that these more or less cancel each other, but such limitations must be recognized when gauging the reliability of the population estimates.

The validity of MRR experiments rests on the assumption that marked individuals behave in every respect as the unmarked ones, and that they mix together in a homogenous, random way. We do not know how marking mosquitoes with dusts might affect their survival and behaviour. Day-Glo powders have been used by other authors (Reisen & Aslamkhan, 1979; Lutwama & Mukwaya, 1994) without any reported effect on survival. Service (1993) could not detect any mortality in hibernating *Culex pipiens* dusted with Saturn Yellow and other Day-Glo fluorescent powders. Further, Touré *et al.* (pers. comm.) observed minimal mortality of marked mosquitoes that were retained in cages inside release huts in Mali, and della Torre and Fortini (pers. comm.) observed no difference in cage mortality of marked and unmarked laboratory mosquitoes. Nonetheless, in view of the importance of this assumption for our conclusions, the possibility that marking affects behaviour must be kept in mind.

It should also be recognized that all conclusions about dispersal and density of *An.gambiae s.l.* in this study depend on the recapture of a small percentage of the population. We recaptured more than 200 mosquitoes, a sizeable number; yet in excess of 20,000 mosquitoes were released. If the recaptures were in some way special – e.g. if certain mosquitoes were captured closer to home because they had been injured – then the analysis might be severely compromised.

Finally, although the results we obtained do seem consistent with other studies on anopheline mosquitoes, there is little information about how these generalize to other locations or to other times at the same location. We observed substantial differences from 1991 to 1992: the population density of *An.gambiae s.l.* during September was estimated to be about 135,000 in 1991, and about 330,000 in 1992; recaptures in neighbouring villages went from 0.09% to 0.21%, and estimated movement within Goundri seemed to decrease, from about 650 m day^{-1} to 350 m day^{-1}. Reasons for this are not evident, though we speculate that environmental factors might have played a role. The experiments in 1992 followed a period of exceptionally heavy rains and flooding. This may have provided good opportunities for breeding, keeping most of the mosquito movement local, but at the same time facilitating occasional inter-village exchange. That would explain why local movement was higher in 1991 but, at the same time, long-distance inter-village movement was less. If this explanation is correct, then further experiments should show a general tendency for long-range dispersal rates to be correlated with mean densities, and sensitive to both climate and geography.

Acknowledgments

This work was based at the Centre National de Lutte contre le Paludisme (CNLP) of Ouagadougou, co-sponsored by the Burkina Faso Ministry of Health and the Italian Ministry of Foreign Affairs Programma di Assistenza Tecnica of the Direzione Generale per la Cooperazione allo Sviluppo. We are indebted to Dr L. Lamizana, Director of CNLP, and to field staff who participated in mosquito collections. We also thank the people of Goundri, without whose collaboration this study would not have been possible. This study is part of a project funded by the European Community under contract No. TS3-CT93-0236. Financial support for C.E.T. was provided by research grant NSF DIR-9024251. Participation of S.G.L. was made possible by a grant from the University of California–Peking University Education Abroad Program. The Day-Glo Color Co., U.S.A., kindly donated fluorescent powders, and ASECNA provided meteorological data in Burkina Faso. The constant support of Dr L. Merzagora and the skilful technical collaboration of Mrs S. Bagalino and G. Croce for PCR analysis are gratefully acknowledged. We thank those who read and commented on the manuscript: Dr J. Brady, Dr J. D. Charlwood, Dr V. Petrarca, Mr S. Schofield and Professor Y. Touré.

References

Blower, J.G., Cook, L.M. & Bishop, J.A. (1981) *Estimating the Size of Animal Populations*. George Allen & Unwin Ltd, London.

Brengues, J. & Coz, J. (1973) Quelques aspects fondamentaux de la biologie d'*Anopheles gambiae* Giles (Sp. A.) et d'*Anopheles funestus* Giles, en zone de savane humide d'Afrique de l'Ouest. *Cahiers O.R.S.T.O.M., Série d'Entomologie Médicale et Parasitologie*, **11**, 107–126.

Clements, A.N. (1963) *The Physiology of Mosquitoes*. Pergamon Press, Oxford.

Clements, A.N. & Paterson, G.D. (1981) The analysis of mortality and survival rates in wild populations of mosquitoes. *Journal of Applied Ecology*, **18**, 373–399.

Collins, F.H. (1994) Prospects for malaria control through the genetic manipulation of its vectors. *Parasitology Today*, **10**, 370–371.

Collins, F.H. & Besansky, N.J. (1994) Vector biology and the control of malaria in Africa. *Science*, **264**, 1874–1875.

Coluzzi, M. (1992) Malaria vector analysis and control. *Parasitology Today*, **8**, 113–118.

Coluzzi, M. & Petrarca, V. (1973) Aspirator with paper cup for collecting mosquitoes and other insects. *Mosquito News*, **33**, 249–250.

Coluzzi, M., Petrarca, V. & Di Deco, M.A. (1985) Chromosomal inversion intergradation and incipient speciation in *Anopheles gambiae*. *Bollettino di Zoologia*, **52**, 45–63.

Coluzzi, M., Sabatini, A., Petrarca, V. & Di Deco, M.A. (1979) Chromosomal differentiation and adaptation to human environments in the *Anopheles gambiae* complex. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, **73**, 483–497.

Costantini, C., Gibson, G., Brady, J., Merzagora, L. & Coluzzi, M. (1993) A new odour-baited trap to collect host-seeking mosquitoes. *Parassitologia*, **35**, 5–9.

Curtis, C.F. (1994) The case for malaria control by genetic manipulation of its vectors. *Parasitology Today*, **10**, 371–374.

Dobzhansky, T., Powell, J.R., Taylor, C.E. & Andregg, M. (1979) Ecological variables affecting the dispersal behavior of *Drosophila pseudoobscura* and its relatives. *The American Naturalist*, **114**, 325–334.

Dobzhansky, T. & Wright, S. (1943) Genetics of natural populations. X. Dispersion rates in *Drosophila pseudoobscura*. *Genetics*, **28**, 304–340.

E.D.S. (1967) *World Weather Records: 1951–1960*. Vol. 5. *Africa*. Environmental Science Services Administration, United States Department of Commerce, Washington, D.C.

Elliott, J.M. (1977) *Some Methods for the Statistical Analysis of Samples of Benthic Invertrebrates*, 2nd edn, Scientific Publication No. 25. Freshwater Biological Association, Ambleside.

Fisher, R.A. & Ford, E.B. (1947) The spread of a gene in natural conditions in a colony of the moth *Panaxia dominula*. *Heredity*, **1**, 143–174.

Gillies, M.T. (1955) The density of adult *Anopheles* in the neighbourhood of an East African village. *American Journal of Tropical Medicine and Hygiene*, **5**, 1103–1113.

Gillies, M.T. (1961) Studies on the dispersion and survival of *Anopheles gambiae* Giles in East Africa, by means of marking and release experiments. *Bulletin of Entomological Research*, **52**, 99–127.

Gillies, M.T. (1980) The role of carbon dioxide in host-finding by mosquitoes (Diptera: Culicidae): a review. *Bulletin of Entomological Research*, **70**, 525–532.

Gillies, M.T. (1988) Anopheline mosquitos: vector behaviour and bionomics. *Malaria. Principles and Practice of Malariology* (ed. by W. H. Wernsdorfer and I. McGregor), Vol. 1, pp. 453–485. Churchill Livingston, Edinburgh.

Gillies, M.T. & Wilkes, T.J. (1965) A study of the age-composition of populations of *Anopheles gambiae* Giles and *A.funestus* Giles in north-eastern Tanzania. *Bulletin of Entomological Research*, **56**, 237–262.

Gillies, M.T. & Wilkes, T.J. (1981) Field experiments with a wind tunnel on the flight speed of some West African mosquitoes (Diptera: Culicidae). *Bulletin of Entomological Research*, **71**, 65–70.

Gupta, S. & Day, K.P. (1994) A strain theory of malaria transmission. *Parasitology Today*, **10**, 476–481.

Hamon, J. (1963) Les moustiques anthropophiles de la région de Bobo-Dioulasso (République de Haute-Volta). Cycles d'agressivité et variations saisonnières. *Annales de la Société Entomologique de France*, **132**, 85–144.

Hamon, J., Coz, J., Adam, J.P., Holstein, M., Rickenbach, A., Brengues, J., Subra, R., Sales, S. & Eyraud, M. (1966) Contribution à l'étude de la répartition des Anopheles en Afrique occidentale. *Cahiers O.R.S.T.O.M., Série Entomologie Medicale*, **4**, 13–70.

Jolly, G.M. (1965) Explicit estimates from capture–recapture data with both birth and immigration: stochastic model. *Biometrika*, **52**, 225–247.

Lawson, G.W. (1966) *Plant Life in West Africa*. Oxford University Press.

Lines, J.D., Lyimo, E.O. & Curtis, C.F. (1986) Mixing of indoor- and outdoor-resting adults of *Anopheles gambiae* Giles s.l. and *Anopheles funestus* Giles (Diptera: Culicidae) in coastal Tanzania. *Bulletin of Entomological Research*, **76**, 171–178.

Linthicum, K.J., Bailey, C.L., Davies, F.G. & Kairo, A. (1985) Observations on the dispersal and survival of a population of *Aedes lineatopennis* (Ludlow) (Diptera: Culicidae) in Kenya. *Bulletin of Entomological Research*, **75**, 661–670.

Lutwama, J.J. & Mukwaya, L.G. (1994) Mark–release–recapture studies on three populations of *Aedes (Stegomyia) simpsoni* complex (Diptera: Culicidae) in Uganda. *Bulletin of Entomological Research*, **84**, 521–527.

Macdonald, D. (1957) *The Epidemiology and Control of Malaria*. Oxford University Press.

Macdonald, W.W., Sebastian, A. & Tun, M.M. (1968) A mark–release–recapture experiment with *Culex pipiens fatigans* in the village of Okpo, Burma. *Annals of Tropical Medicine and Parasitology*, **62**, 200–209.

Manga, L., Fondjo, E., Carnevale, P. & Robert, V. (1993) Importance of low dispersion of *Anopheles gambiae* (Diptera, Culicidae) on malaria

transmission in hilly towns in South Cameroon. *Journal of Medical Entomology*, **30**, 936–938.

Merzagora, L. (1993) Variazioni ecologiche ed epidemiologia della malaria in una zona di savana sudanese presso Ouagadougou, Burkina Faso. Ph.D. thesis, Università 'La Sapienza', Rome.

Molineaux, L. & Gramiccia, G. (1980) *The Garki Project. Research on the Epidemiology and Control of Malaria in the Sudan Savanna of West Africa*. World Health Organization, Geneva.

Paskewitz, S.M. & Collins F.H. (1990) Use of the polymerase chain reaction to identify mosquito species of the *Anopheles gambiae* complex. *Medical and Veterinary Entomology*, **4**, 367–373.

Petrarca, V., Petrangeli, G., Rossi, P. & Sabatinelli, G. (1986) Étude chromosomique d'*Anopheles gambiae* et *Anopheles arabiensis* à Ouagadougou (Burkina Faso) et dans quelques villages voisins, *Parassitologia*, **28**, 41–61.

Press, W.H., Teukolsky, S.A., Vetterling, W.T. & Flannery, B.P. (1992) *Numerical Recipes in C: The Art of Scientific Computing*, 2nd edn. Cambridge University Press.

Quiñones, M.L. (1991) Movements of *Anopheles gambiae s.l.* between neighbouring villages in The Gambia. M.Sc. thesis, University of London.

Rawlings, P., Curtis, C.F., Wickramasinghe, M.B. & Lines, J. (1981) The influence of age and season on dispersal and recapture of *Anopheles culicifacies* in Sri Lanka. *Ecological Entomology*, **6**, 307–319.

Reisen, W.K. & Aslamkhan, M. (1979) A release–recapture experiment with the malaria vector, *Anopheles stephensi*, Liston with observations on dispersal, survivorship, population size, gonotrophic rhythm and mating behaviour. *Annals of Tropical Medicine and Parasitology*, **73**, 251–269.

Robert, V. & Carnevale, P. (1991) Influence of deltamethrin treatment of bed nets on malaria transmission in the Kou Valley, Burkina Faso. *Bulletin of the World Health Organization*, **69**, 735–740.

Rudd, W.G. & Gandour, R.W. (1985) Diffusion model for insect dispersal. *Journal of Economic Entomology*, **78**, 295–301.

Sabatinelli, G., Rossi, P. & Belli, A. (1986) Étude sur la dispersion d'*Anopheles gambiae* s.l. dans une zone urbaine à Ouagadougou (Burkina Faso). *Parassitologia*, **28**, 33–39.

Scott, J.A., Brogdon, W.G. & Collins, F.H. (1993) Identification of single specimens of the *Anopheles gambiae* complex by the polymerase chain reaction. *American Journal of Tropical Medicine and Hygiene*, **49**, 520–529.

Service, M.W. (1993) *Mosquito Ecology: Field Sampling Methods*, 2nd edn. Elsevier Applied Science Publishers Ltd, London.

Taylor, C.E., Jefferson, D. & Burla, H. (1987) Habitat-dependent dispersal of *Drosophila obscura* and *D. subobscura*. *Genética Ibérica*, **39**, 547–563.

Taylor, C.E. & Powell, J.R. (1983) Population structure of *Drosophila*: genetics and ecology. *Biology and Genetics of Drosophila* (ed. by M. Ashburner, H. L. Carson and J. N. Thompson), Vol. 3, pp. 29–59. Academic Press, New York.

Taylor, C.E., Toure, Y.T., Coluzzi, M. & Petrarca, V. (1993) Effective population size and persistence of *Anopheles arabiensis* during the dry season in West Africa. *Medical and Veterinary Entomology*, **7**, 351–357.

Thomson, M.C., Connor, S.J., Quiñones, M.L., Jawara, M., Todd, J. & Greenwood, B.M. (1995) Movement of *Anopheles gambiae s.l.* malaria vectors between villages in the Gambia. *Medical and Veterinary Entomology*, **9**, 413–419.

W.H.O. (1991) Report of the meeting 'Prospects for malaria control by genetic manipulation if its vectors', 27–31 January 1991. Unpublished document TDR/BCV/MAL–ENT/91.3 (World Health Organization, Geneva.)

White, G.B. (1974) *Anopheles gambiae* complex and disease transmission in Africa. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, **68**, 278–301.

Wright, S. (1978) *Evolution and the Genetics of Populations*, Vol. IV. *Variability Within and Among Natural Populations*. University of Chicago Press.

Accepted 25 Feburary 1996