



Localized breeding of the *Anopheles gambiae* complex (Diptera: Culicidae) along the River Gambia, West Africa

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Abstract

A study was undertaken to identify the major larval habitats of the *Anopheles gambiae* (Giles) complex in rural Gambia. Mosquito larvae and pupae were sampled along transects and in specific habitats in the central region of the country during the rainy seasons of 1996 and 1997. The sampling showed that the major breeding sites were located on the flooded alluvial soils bordering the river. The largest numbers of larvae were found during September, one month after the peak rains. Polymerase chain reaction analysis of specimens showed that *Anopheles melas* (Theobald) was the dominant species in the flooded areas (81.5%), followed by *A. gambiae* sensu stricto (Giles) (18.0%) and *A. arabiensis* (Patton) (0.5%). By sampling in specific habitats it was evident that *A. arabiensis* was mainly breeding in rain-fed rice fields along the edge of the alluvial soils. *Anopheles melas* and *A. gambiae* s.s. often coexisted but whereas *A. melas* were found in water with a salinity of up to 72‰ sea water (25.2 g NaCl l⁻¹), *A. gambiae* s.s. only occurred in water with up to 30‰ sea water (10.5 g NaCl l⁻¹). *Anopheles melas* larvae were found in association with plant communities dominated by sedges and grasses (*Eleocharis* sp., *Paspalum* sp., *Sporobolus* sp.) and sea-purslane *Sesuvium portulacastrum* (L.) and the presence of cattle hoof prints, whereas *A. gambiae* s.s. larvae mainly occurred in association with *Paspalum* sp. and *Eleocharis* sp. The study showed that even during the peak rainy season, breeding of the *A. gambiae* complex is almost entirely restricted to the extensive alluvial areas along the river.

Introduction

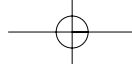
Malaria transmission in the Sahel region of Africa is characterized by often intense seasonal transmission because of the brief, but often heavy rainfall. Large geographical

differences are seen in the epidemiology of malaria in the region and even between villages a few kilometres apart (Vercruyse, 1985; Julvez *et al.*, 1992, 1997; Alonso *et al.*, 1993; Touré *et al.*, 1996; Thomson *et al.*, 1996; Thomas & Lindsay, 2000; Clarke *et al.*, 2002). To understand the reasons behind these geographical variations in transmission dynamics, it is essential to determine where and when the vector mosquitoes are breeding and describe the characteristics of their breeding habitats.

The Gambia lies in the Sahel region of West Africa, where the climate is characterized by a short rainy season from

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June to October, with an annual rainfall of $\approx 600\text{--}800$ mm. The most important malaria vectors are *Anopheles gambiae* sensu stricto (Giles) *Anopheles melas* (Theobald) and *Anopheles arabiensis* (Patton) (Diptera: Culicidae) (Bryan, 1983; Lindsay *et al.*, 1993), all members of the *A. gambiae* complex (Gillies & Coetzee, 1987). A considerable amount of research has been carried out on adult mosquitoes in this country but only two studies have investigated the breeding of mosquito larvae. Bertram *et al.* (1958), working on the coast, found freshwater *A. gambiae* sensu lato breeding near a small stream and in puddles formed by car tracks. *Anopheles melas* was found breeding in saline flooded areas with sea-purslane *Sesuvium portulacastrum* L. (Aizoaceae) and beneath or near white mangrove *Avicennia* sp. (Avicenniaceae). A later study by Thomas and Lindsay (2000) found that the highest density of larvae was found on the landward edge of the extensive areas of pooled sediment bordering the River Gambia. However, in this study collections were carried out at one point in time during the rainy season (August, 1995) and the *A. gambiae* larvae collected were not identified to sibling species level.

More extensive studies of the breeding of the *A. gambiae* complex have been carried out in other West African countries, including Sierra Leone (Ribbands, 1944b; Thomson-Muirhead, 1945; Ford Tredre, 1946), Liberia (Gelfand, 1955) and Nigeria (Barber *et al.*, 1931; Chwatt, 1949). The ecology of these study sites resembles The Gambia in having riverine ecosystems affected by saltwater intrusion but they are all located outside the Sahel region and have much higher annual rainfall. These accounts describe the larval ecology of *A. melas* and fresh water breeding *A. gambiae* s.l. The fresh water breeding *A. gambiae* s.l. were found on the landward edge of floodplains whereas the salt-tolerant species *A. melas* was most commonly associated with saline grass covered floodplains and extensive orchards of white mangrove (*Avicennia* sp.) (Barber *et al.*, 1931; Ribbands, 1944b; Thomson-Muirhead, 1945; Gelfand, 1955). None of the larval studies from West Africa separated the freshwater breeding *A. gambiae* sibling species into *A. gambiae* s.s. and *A. arabiensis*. However, both are known to breed in open sunlit freshwater pools (Gillies & Coetzee, 1987).

The malaria transmission season in The Gambia is brief but intense from July to the beginning of December, when the mosquito populations decline rapidly (Lindsay *et al.*, 1993; Hemingway *et al.* 1995). The entomological inoculation rate per transmission season varies enormously within the study area and ranges from less than one to more than 165 infective bites (Bøgh *et al.*, 1999), with the highest transmission rates being found nearest the river (Bøgh *et al.*, 1999; Thomas & Lindsay, 2000).

This study aimed to describe the geographical and seasonal variation in the breeding of different members of the *Anopheles gambiae* complex in The Gambia. It is part of a larger study describing the ecology of malaria in the central part of the country (Bøgh, 1999; Bøgh *et al.*, 2001; Clarke, 2001).

Materials and methods

Study area

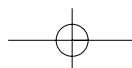
The country is dominated by the River Gambia, which is characterized by saltwater intrusions in its lower reaches caused by tidal differences. The flow of the river is highly seasonal and depends largely on the precipitation in the Futa

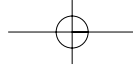
Jallon highlands in Guinea. During the dry season, the salt front can travel 200 km up river, creating large areas of salt marsh and mangrove forests near the river. Only during the rainy season is the outflow of fresh water so high that river and adjacent flooded areas become completely or partly non-saline (Sylla *et al.*, 1995). The soil structure of The Gambia is characterized by two main types: sandstone inlands where most of the villages and farms are located; and alluvial deposits along the river (Trolldalen, 1991). Descriptions of the physical and chemical composition of the swamp soils have been made by Giglioli & Thornton (1965).

The study area covered approximately 2500 km² and was located in the central part of the country, extending from 50 km east to 50 km west of Farafenni town (1500200N, 435500E). Co-ordinates are given in Universal Transverse Mercator (UTM) grid metres from UTM zone 28. Figure 1 illustrates the study area which was bounded by the northern and southern border to Senegal and the UTM meridians (410000E) and (480000E). To identify the major mosquito breeding sites, transects were established at four different sites along the river (see fig. 1). Two sites were chosen in the west to describe the breeding in more saline habitats and two sites in the east to cover the habitats less dominated by seawater. Each transect started at the periphery of a village near the floodplains. The selected villages were Jumansari Koto (UTM: 1493300N, 420500E), and Samba Soto (UTM: 1503500N, 456500E) on the north bank and Toniataba (UTM: 1486000N, 437200E) and Sowe Kunda (UTM: 1497300N, 466600E) on the south bank. Each transect began from the house nearest the river or major tributary and continued directly towards the nearest waterway. Compass bearings for the transects were taken from survey maps (DOS, 1974) and used in the field with a hand-held compass. The distance from the starting point was measured with a manual odometer but during the peak of the rainy season the mud became so sticky that it was impossible to use. During this period the distance was estimated by counting the number of paces between collection points. The precise location of each transect was determined during 1997 with the use of a hand-held, differential Global Positioning System (GPS) receiver (Geoplorator II®, Trimble Navigation Limited, California, USA) which had an accuracy of about 5 m.

Larval collections along transects

During 1996, transects were surveyed in July, September and October, except for transect 3 and 4 where surveys were not carried out in July. During 1997 all four transects were surveyed in August, October and November. Measurements were made every 100 m along the transects and additionally at the edges of any water collections or streams crossing the transect. Sampling continued along the transects towards the river until further progress was impossible due to deep water or dense mangrove forest. At each collection site, dipping was delayed for 3 min to let the mosquito larvae surface after the disturbance of the water. A total of ten dips were taken within a 5 m radius using a 350 ml WHO standard dipper. Sampling was done by sampling purposely among plants and roots to catch the maximum number of larvae at any site. All instars and pupae of anopheline larvae were carefully collected from each scoop, counted and then transferred to a small plastic container for later species identification.



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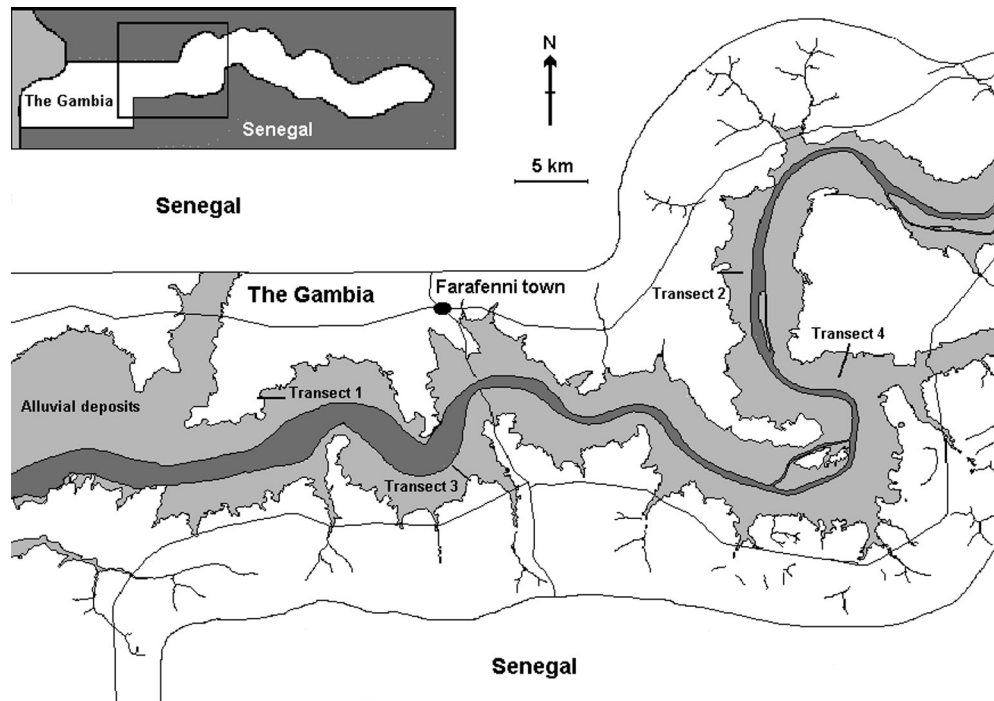


Fig. 1. The study area in the central part of The Gambia including the position of the four larval transects surveyed during 1996 and 1997. The river is shown in dark grey and the floodplain in light grey. Solid lines within The Gambia indicate major roads.

Larval collection in specific habitats

To confirm that the transects were representative of the study area, larval sampling was also carried out in a variety of aquatic habitats in different parts of the study area during the rainy seasons of 1996 and 1997. Sampling was focused in the floodplains and in the natural depressions on the periphery or outside areas with alluvial deposits. If a water body was located, sampling was purposely carried out with up to 20 dips at each site. At each site the presence or absence of anophelines and vegetation characteristics were recorded. All instars of anopheline larvae were collected from each scoop, counted and then transferred to a small plastic container for later species identification (see below).

Environmental measurements

At all sites where dipping took place, the depth of water, salinity and surface characteristics were recorded. Salinity was measured using a salinity meter (M30/10 FT, YSI Inc. Ohio, USA). The land surface types were classified into the following main categories:

1. Upland agriculture
2. Forest
3. Upland grassland
4. Barren mudflat
5. Barren mudflat with hoof prints
6. Mudflat dominated by spike-rush *Eleocharis* sp. (Cyperaceae)
7. Mudflat dominated by paspalum *Paspalum* sp. (Poaceae)
8. Mudflat dominated by sea grass *Sporobolus* sp. (Poaceae)

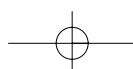
9. Mudflat dominated by swamp rice *Oryza sativa* (L.) (Poaceae)

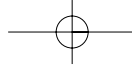
10. Mudflat dominated by sea-purslane *Sesuvium portulacastrum* (Aizoaceae).

Specimens were taken of predominant plant species and preserved for later identification at the Botanical Museum and Library, University of Copenhagen, Denmark.

Species identification

In the laboratory, larvae were transferred to 96% ethanol for later identification. Since nearly all malaria in The Gambia is transmitted by members of the *A. gambiae* complex (Bryan, 1983; Lindsay *et al.*, 1989, 1993), species identification was performed using a polymerase chain reaction (PCR) technique specific for this group of mosquitoes (Scott *et al.*, 1993). The primers used were for *A. gambiae* s.s., *A. melas* and *A. arabiensis*, which are the only known members of the complex present in The Gambia (Bryan *et al.*, 1982). DNA was extracted from first instar larvae through to pupae and analysed twice for presence of *A. gambiae* complex DNA. If a specimen was negative in both PCR tests it was classified as a non-member of the *A. gambiae* complex. When more than 30 larvae were caught at one sampling location only the first 30 randomly selected larvae were identified by PCR and the total number of larvae of a given species calculated from the proportion of analysed specimens and the total number of caught larvae. Fourteen larval containers from 1996 were spoilt during transport and could not be identified to species level. These samples were only included in the part of the analysis presenting the total annual catches along the four transects.





Geographical information system

A geographical information system (GIS) was constructed on the basis of 1:50,000 survey maps (DOS, 1974). These maps were originally developed from aerial photography and include the outline of the main types of land cover along the river. Maps were digitized using ArcInfo® (ESRI, California, USA) and measurements of distances from the floodplain edge done using Arcview® (ESRI, California, USA).

Statistical analysis

Data entry was done in DBASE IV® (Borland International, California, USA) software and statistical analysis using SPSS® software (version 9.0, SPSS Inc., Chicago, USA). The total number of each species caught in ten dipo was recorded and recalculated as geometric means (GM) to adjust for the skewed distribution of mosquito larvae. Discriminant analysis was used to identify associations between land surface classes and the presence or absence of the different species of mosquito larvae. The analysis was based on the presence or absence of larvae in a given habitat using the combined transect data sets from 1996 and 1997.

Results

Larval catches along transects

The major habitats near the River Gambia are shown schematically in fig. 2. The general profile of the transects walked from a village was first an area of farmland followed by a narrow strip of forest. This led to an open area of alluvial deposits of which the first part normally consisted of barren dry mud flats followed by flooded mud flats with large areas of sea grass (*Sporobolus* sp.), spike-rush (*Eleocharis* sp.) and sea-purslane (*Sesuvium portulacastrum*). Finally, there were white and red mangrove trees (*Avicennia* sp. and *Rhizophora* sp. (Rhizophoraceae)) bordering saline sections of the River Gambia and its major tributaries.

The water depth and species composition of the larvae collected along the four transects in 1996 and 1997 is presented in fig. 3. Transects 1, 2 and 4 were little affected by daily tides but transect 3 was affected substantially by the tide due to its proximity to the river. The average water level along transect 3 was higher in 1996 compared to 1997 because sampling by chance was carried out during high tides in 1996. There were also large differences in salinity along the transects. Transect 1 had the highest level with an average of 27.6% (95% CI: 24.8–30.3%) sea water compared to only 3.4% (1.7–5.0%) along transect 2, 9.2% (6.6–11.8%) along transect 3 and 13.5% (10.3–16.6%) along transect 4. These differences in salinity did not reflect the distance from the ocean (i.e. salt front) but rather the combined result of freshwater out-flux, distance from river, evaporation and soil salt saturation. There was considerable variation in

mosquito breeding among transects and between years. However, larval breeding generally took place at the same sites along the transects each year and the species composition of the larvae was also generally consistent between years.

Larval breeding over the rainy season

The seasonal variation in larval density along the transects in 1996 and 1997 is shown in figure 4. This shows that most breeding took place in September, about a month after the peak rainy season, and continued after the rains stopped in October. These findings also suggest that *A. melas* breeding started earlier than *A. gambiae* s.s. and continued for a longer period after the rains had stopped. However, this apparent difference may be an artefact of differential detection rates for the different sibling species caused by the limitations of sampling low densities of larvae.

Location of the species-specific breeding sites

Figure 5 illustrates the total geometric mean (GM) number of *A. gambiae* s.s. and *A. melas* larvae collected along all four transects in both 1996 and 1997 in relation to the edge of the alluvial deposits. This also shows how open surface water was confined to the alluvial deposits. The GM number of *A. gambiae* s.s. per ten dipo was 0.09 (95% CI: 0.01–0.16) larvae and 0.55 (0.099–1.00) per ten dipo for *A. melas*. The highest larval densities of both sibling species were seen close to the edge of the floodplains although high larval densities continued to be recorded more than a kilometre into the alluvial flood plains. Along the transects *A. arabiensis* was only found on one occasion in 1997 about 400 m into the flooded areas on transect 4.

Larval breeding and salinity

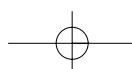
Figure 6 illustrates the range of salinity where *A. gambiae* s.s. and *A. melas* larvae were found. *Anopheles gambiae* s.s. and *A. melas* were often found co-existing in the habitats but whereas *A. gambiae* s.s. larvae only occurred in up to 30% sea water (10.5 g NaCl l⁻¹), *A. melas* were caught at salinities as high as 72% sea water (25.2 g NaCl l⁻¹). On the one occasion where *A. arabiensis* larvae were found along the transects, this was in 12% sea water (4.2 g NaCl l⁻¹).

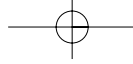
Plant species markers for larval breeding

The relationships between dominant plant species and land surface types and the presence of either *A. gambiae* s.s. or *A. melas* are shown in table 1. A total of 365 sampling sites was included in the discriminant analysis using ten land surface classes for both mosquito species. There were too few *A. arabiensis* caught for this type of analysis. The presence of *Eleocharis* sp. and *Paspalum* sp. were both key indicators for the breeding of *A. gambiae* s.s. and *A. melas*. In



Fig. 2. A cross-sectional view of the floodplains in the central part of The Gambia.



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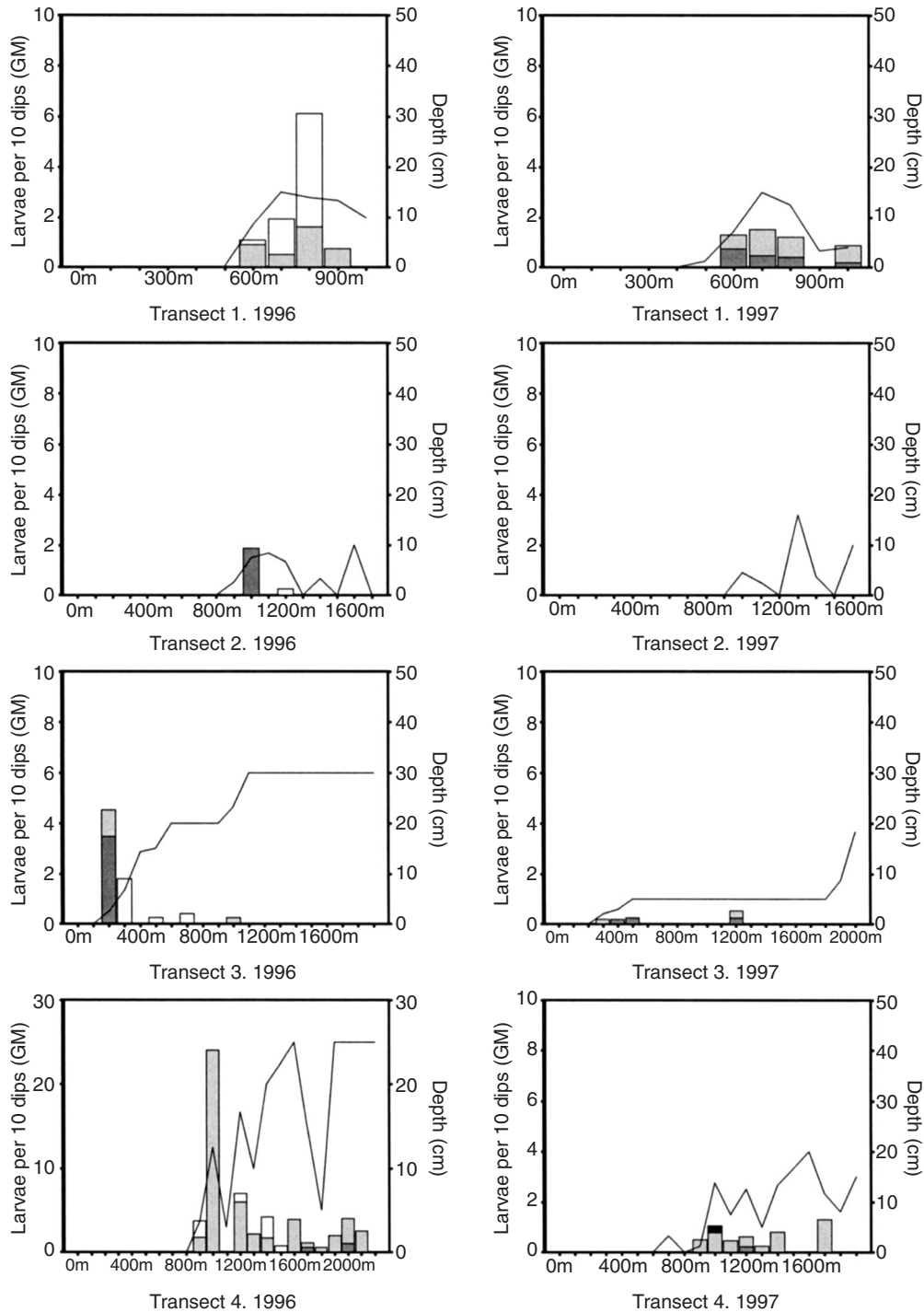
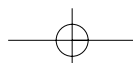


Fig. 3. The geometric mean (GM) number of *Anopheles gambiae* complex larvae caught along four transects moving from the edge of a village into the floodplain area in 1996 and 1997. The mean water level along the transects is presented in centimetres. *A. gambiae* s.s. (■); *A. melas* (□); *A. arabiensis* (■); unidentified (□).

addition, *A. melas* was also found associated with *Sporobolus* sp., *Sesuvium portulacastrum* and hoof prints in the mud flats. Anopheline larvae were never found on the farmland and grasslands around the villages or in the forests near the alluvial deposits.

Results of larval collections outside the transects

Results of larval catches outside the transects during 1996 and 1997 are presented in table 2. Collections from flooded grass and sedge habitats inside the floodplains were



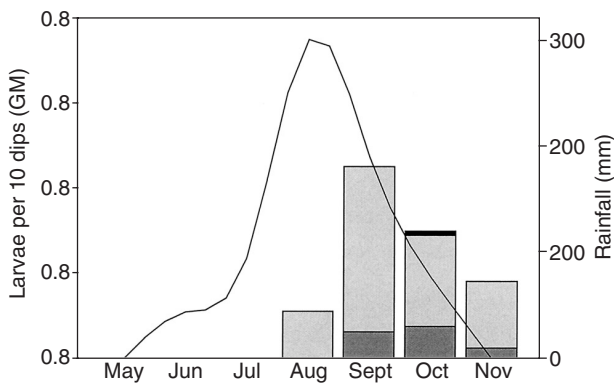
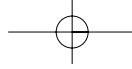


Fig. 4. The average monthly rainfall in 1996 and 1997 and the bi-annual geometric mean (GM) number of *Anopheles gambiae* s.s. (■), *A. melas* (□) and *A. arabiensis* (■) larvae caught per ten dips.

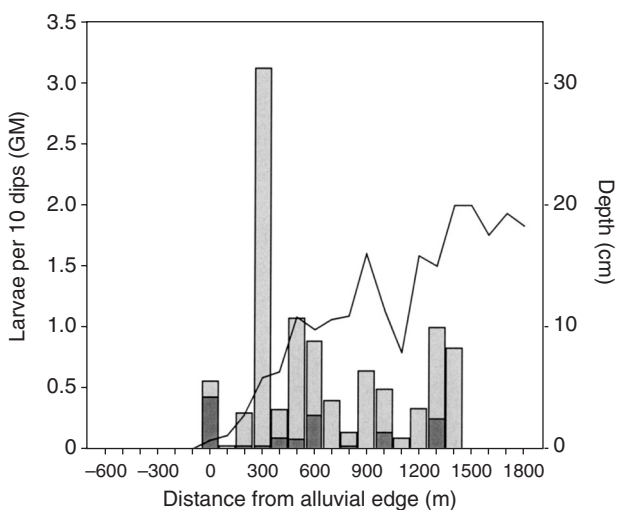


Fig. 5. The total geometric mean number of *Anopheles gambiae* s.s. (■) and *A. melas* (□) larvae collected along all four transects in 1996 and 1997 in relation to the edge of the alluvial soils (0 m). Negative distances are inland areas, positive distances are alluvial, often continuously flooded areas. The mean water level along the transects is presented in centimetres.

dominated by *A. melas* and *A. gambiae* s.s. with a few *A. arabiensis* confirming the findings from the transects. Rain-fed rice fields, common in alluvial creeks far from the river, were dominated by anopheline species not belonging to the *A. gambiae* complex. However, these rain-fed rice fields did have the highest density of *A. arabiensis* compared to any other aquatic habitat.

Discussion

The findings on the breeding of *A. gambiae* s.s., *A. melas* and *A. arabiensis* in the central part of The Gambia both

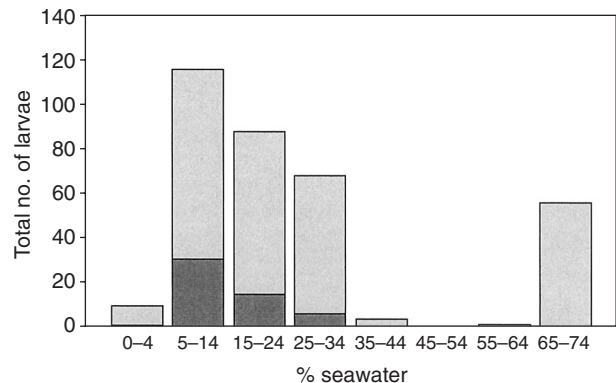
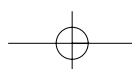


Fig. 6. The total number of *Anopheles gambiae* s.s. (■) and *A. melas* (□) larvae caught at different levels of salinity in the study area.

support and expand the knowledge from previous work on the breeding behaviour of these species. Most larvae were caught in September, just after the peak rainy season, when the alluvial soils were flooded with relatively fresh water. This is consistent with the results from adult collections, which show a similar seasonal pattern (Bøgh *et al.*, 1999). Most breeding took place within the first kilometre of the floodplains but high densities of larvae were found as far as 1400 m from the edge of the alluvial soils. This is most likely the result of active flight and oviposition by female mosquitoes. Eggs or larvae are unlikely to be transported this far by water flow since in transect 3, which was most affected by tides, the larvae were no greater dispersed than in the other transects. It is possible that breeding occurs even further into the floodplains, provided a suitable habitat is present. The highest density of anopheline mosquito larvae was found amongst dense vegetation, and only rarely in the free water surface. This could indicate that the adult females may use the plant species for guidance when laying their eggs. Laboratory studies further indicate that predation by fish is less frequent when the larvae lie close to grass shoots emerging from the water (S.W. Lindsay, unpublished data).

Anopheles melas was the most abundant species breeding in the flooded alluvium, comprising 81.5% of the *A. gambiae* complex larvae sampled, followed by 18% *A. gambiae* s.s. and 0.5% *A. arabiensis*. This contrasted with the findings from indoor catches of adult populations in the area where 70% were *A. gambiae* s.s., 20% *A. melas* and 10% *A. arabiensis* (Bøgh *et al.*, 2001). This apparent contradiction reflects the more zoophilic and exophilic behaviour of *A. melas* and the highly endophilic and anthropophilic habits of *A. gambiae* s.s. (Gillies & DeMeillon, 1968). Thus although *A. melas* predominates in the riparian breeding sites, *A. gambiae* s.s. is the principal vector of malaria in the area (Lindsay *et al.*, 1993; Hemingway *et al.*, 1995). The main breeding habitats of *A. melas* were found in flooded areas with vegetation dominated by *Sporobolus* sp., *Eleocharis* sp., and *Sesuvium* sp. resembling findings from Liberia (Gelfand, 1955) and Nigeria (Barber *et al.*, 1931; Chwatt, 1945). The only exception to this finding was in Sierra Leone, where *A. melas* was found breeding under large stands of white mangrove (*Avicennia* sp.) (Thomson-Muirhead, 1945). Breeding in cattle hoof prints occurred where the salty mud flats became



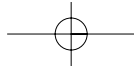


Table 1. Results of discriminant analysis showing the vegetation and land surface types that are associated with the breeding of *Anopheles gambiae* s.s and *Anopheles melas* and the strength of the derived models in predicting presence of larvae based on the surface types.

<i>Anopheles gambiae</i> s.s.	
Variable	Correlation
<i>Paspalum</i> sp.	0.811
<i>Eleocharis</i> sp.	0.791

Correct classification: 80.5% (canonical correlation 0.25, Wilks' lambda 0.94, $P < 0.001$)

<i>Anopheles melas</i>	
Variable	Correlation
<i>Eleocharis</i> sp.	0.700
<i>Paspalum</i> sp.	0.633
<i>Sesuvium</i> sp.	0.374
<i>Sporobolus</i> sp.	0.210
Hoof prints	0.204

Correct classification: 82.7% (canonical correlation 0.47, Wilks' lambda 0.78, $P < 0.001$)

partly flooded, creating thousands of small isolated breeding sites protected from aquatic predators. That *A. melas* larvae were found in association with several vegetation and surface types illustrates their less restricted choice of breeding habitat within the floodplains. *Anopheles melas* is a well known salt water breeding mosquito, and was found in salinities up to 72% sea water, although it can develop successfully in 200% sea water (Ribbands, 1944a). Collections of *A. melas* larvae in water with less than 5% sea water, show that *A. melas* breeds in a wide spectrum of salinities in nature. Since Gelfand (1955) found that adult *A. melas* are unable to distinguish between different salinities, the association with specific plant types suggests that the mosquitoes may use these for guidance for ovipositioning sites.

The highest densities of *A. gambiae* s.s. larvae were found near the edge of the floodplain area. This supports the findings of Muirhead-Thomson (1945) in Sierra Leone who described freshwater *A. gambiae* s.l. breeding near the landward edges of the floodplains. *Anopheles gambiae* s.s. larvae were, however, also found at high densities up to 1300 m into the flooded alluvial soils illustrating that they breed in most of the flooded areas as long as a suitable habitat is present. Although *A. gambiae* s.s. larvae are typically associated with freshwater, larvae were found in

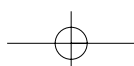
water up to 30% sea water, which is close to the upper limit of tolerance of 37.5% found under laboratory conditions for freshwater *A. gambiae* s.l. (probably *A. gambiae* s.s.) (Ribbands, 1944a). To our knowledge this is the first time *A. gambiae* s.s. has been described at such high salinities in nature, showing that *A. gambiae* s.s. do breed in mildly brackish waters. The highest number of *A. gambiae* s.s. larvae were, however, found just after the peak rainy season when water salinity was at its lowest. *Anopheles gambiae* s.s. were found breeding in association with the grass *Paspalum* sp. and the spike-rush *Eleocharis* sp. *Sporobolus* sp. is abundant along the edges of the floodplains, whereas *Eleocharis* sp. is found in more constantly flooded areas further into the floodplains. *A. gambiae* s.s. and *A. melas* often coexisted in the same sites. This phenomenon may have been enhanced by the water movements and changing salinity caused by the rains and tidal changes. Whilst some inter-species competition may occur it is clearly not enough to exclude coexistence of the two species. Presumably *A. gambiae* s.s. and *A. melas* have overlapping larval habitats and the immediate saltwater concentration defines which of the two species will be the most successful competitor.

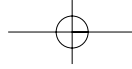
Collections from outside the transects confirmed that the larval habitats on the flooded alluvium are dominated by *A. melas* and *A. gambiae* s.s., with occasional breeding of *A. arabiensis*. It was expected that the rain-fed rice fields on the edge or just outside the alluvium would be important breeding sites not covered by the transect collections. The catches from these sites, however, suggest that they are of only minor importance for *A. gambiae* s.s. and *A. melas*, but are the main habitat for *A. arabiensis*, since this species was found in relatively high numbers in this habitat. These findings suggest that the main breeding habitat for *A. arabiensis* is not in the large flooded areas but in the more temporary rain-fed pools on the periphery of the alluvial deposits. High densities of adult *A. arabiensis* have previously been described near irrigated rice fields in The Gambia during the dry season (Lindsay *et al.*, 1991).

In conclusion, this study demonstrates that almost all breeding of the *A. gambiae* complex takes place within the flooded alluvial deposits along the river. There is simply very little free surface water outside these areas, even after heavy rainfall, since most of the water quickly filters away on the highly porous sandy soils away from the river. Larval breeding is not limited to the periphery of the alluvial deposits but occurs throughout the flooded area outside the mangrove forest. The lack of breeding outside the alluvial area explains why there is a very sharp gradient in adult mosquito density when moving away from the flooded areas (Lindsay *et al.*, 1993; Thomson *et al.*, 1996; Bøgh *et al.*, 1999; Thomas & Lindsay, 2000). Although this study was

Table 2. The numbers of anopheline larvae caught in various breeding habitats outside the transects and the relative distribution of the *Anopheles gambiae* complex sibling species among the caught larvae.

Vegetation class	No. sites	No. larvae identified	% <i>A. gambiae</i> s.s.	% <i>A. melas</i>	% <i>A. arabiensis</i>	% Other anophelines
Grass in flood plains	6	63	35	33	2	30
Sedge in flood plains	7	96	18	44	0	38
Rain-fed rice fields	8	111	5	1	4	90
Rice nursery	1	29	59	0	0	41
Swamp rice	1	4	0	0	0	100





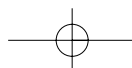
done in an area affected by salt-water intrusion, it is likely that similar breeding patterns exist along other flood-prone river systems in the Sahel region of Africa. Despite these areas covering only a small proportion of the landmass of Sahelian Africa, they account for a disproportionately large part of the malaria transmission in the region.

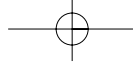
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References

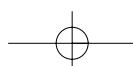
- Alonso, P.L., Lindsay, S.W., Armstrong, S.J., Gomez, P., Hill, A.G., David, P.H., Fegan, G., Cham, K. & Greenwood, B.M. (1993) A malaria control trial using insecticide-treated bed nets and targeted chemoprophylaxis in a rural area of The Gambia, West Africa. 2. Mortality and morbidity from malaria in the study area. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **87** Suppl 2, 13–17.
- Barber, M.A., Olinger, M.T. & Putnam, P. (1931) Studies on malaria in southern Nigeria. *Annals of Tropical Medicine and Parasitology* **25**, 461–501.
- Bertram, D.S., McGregor, I.A. & McFadzean, J.A. (1958) Mosquitoes of the colony and protectorate of The Gambia. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **52**, 135–151.
- Bryan, J.H. (1983) *Anopheles gambiae* and *A. melas* at Brefet, The Gambia, and their role in malaria transmission. *Annals of Tropical Medicine and Parasitology* **77**, 1–12.
- Bryan, J.H., Di Deco, M.A., Petrarca, V. & Coluzzi, M. (1982) Inversion polymorphism and incipient speciation in *Anopheles gambiae* s. str. in The Gambia, West Africa. *Genetica* **59**, 167–176.
- Bøgh, C. (1999) *Variation in malaria transmission in rural Gambia*. 118 pp. PhD thesis, University of Copenhagen.
- Bøgh, C., Clarke, S.E., Thomas, C.J. & Lindsay, S.W. (1999) Sharp decline in malaria transmission away from river systems in The Gambia. pp. 88–102 in *Variation in malaria transmission in rural Gambia*. PhD thesis (Bøgh, C.), University of Copenhagen.
- Bøgh, C., Clarke, S.E., Pinder, M., Sanyang, F. & Lindsay, S.W. (2001) Effect of passive zooprophylaxis on malaria transmission in The Gambia. *Journal of Medical Entomology* **38**, 822–828.
- Chwatt, L.J. (1945) Studies on the melanic variety of *Anopheles gambiae* in southern Nigeria. *Journal of Tropical Medicine and Hygiene* **48**, 22–30.
- Chwatt, L.J. (1949) *Anopheles gambiae melas* control by swamp drainage in a coastal zone of Nigeria, British West Africa. *Mosquito News* **9**, 56–69.
- Clarke, S.E. (2001) *Variation in malaria risk and response in rural Gambia*. 162 pp. PhD thesis, University of Copenhagen.
- Clarke, S.E., Bøgh, C., Brown, R.C., Walraven, G.E.L., Thomas, C.J. & Lindsay, S.W. (2002) Risk of malaria attacks in Gambian children is greater away from malaria vector breeding sites. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **96**, 499–506.
- DOS (1974) Survey maps of The Gambia, 1:50,000. Directorate of Overseas Surveys, United Kingdom. Stanford Ltd., London, UK.
- Ford Tredre, R. (1946) The role of *Anopheles gambiae* var. *melas* in the transmission of malaria in the vicinity of Freetown estuary, Sierra Leone, 1943. *Annals of Tropical Medicine and Parasitology* **40**, 380–420.
- Gelfand, H.M. (1955) *Anopheles gambiae* Giles and *Anopheles melas* Theobald in a coastal area of Liberia, West Africa. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **49**, 508–527.
- Giglioli, M.E.C. & Thornton, I. (1965) The mangrove swamps of Keneba, Lower Gambia River Basin. I. Descriptive notes on the climate, the mangrove swamps and the physical composition of their soils. *Journal of Applied Ecology* **2**, 81–103.
- Gillies, M.T. & Coetzee, M. (1987) *A supplement to the Anophelinae of Africa South of the Sahara*. The South African Institute for Medical Research, Johannesburg.
- Gillies, M.T. & DeMeillon, B. (1968) *The Anophelinae of Africa south of the Sahara (Ethiopian zoogeographical region)*. The South African Institute for Medical Research, Johannesburg.
- Julvez, J., Develoux, M., Mounkaila, A. & Mouchet, J. (1992) Diversity of malaria in the Sahelo-Saharan region. A review apropos of the status in Niger, West Africa. *Annales de la Société Belge de Médecine Tropicale* **72**, 163–177.
- Julvez, J., Mouchet, J., Michault, A., Fouta, A. & Hamidine, M. (1997) Eco-epidemiology of malaria in Niamey and in the river valley, the Republic of Niger, 1992–1995. *Bulletin de la Société de Pathologie Exotique* **90**, 94–100.
- Hemingway, J., Lindsay, S.W., Small, G.J., Jawara, M. & Collins, F.H. (1995) Insecticide susceptibility status in individual species of the *Anopheles gambiae* complex (Diptera: Culicidae) in an area of The Gambia where pyrethroid impregnated bednets are used extensively for malaria control. *Bulletin of Entomological Research* **85**, 229–234.
- Lindsay, S.W., Shenton, F.C., Snow, R.W. & Greenwood, B.M. (1989) Responses of *Anopheles gambiae* complex mosquitoes to the use of untreated bednets in The Gambia. *Medical and Veterinary Entomology* **3**, 253–262.
- Lindsay, S.W., Wilkins, H.A., Zieler, H.A., Daly, R.J., Petrarca, V. & Byass, P. (1991) Ability of *Anopheles gambiae* mosquitoes to transmit malaria during the dry and wet season in an area of rice cultivation in The Gambia. *Journal of Tropical Medicine and Hygiene*, **94**, 313–324.
- Lindsay, S.W., Alonso, P.L., Armstrong, S.J., Hemingway, J., Thomas, P.J., Shenton, F.C. & Greenwood, B.M. (1993) A malaria control trial using insecticide-treated bed nets and targeted chemoprophylaxis in a rural area of The Gambia, West Africa. 3. Entomological characteristics of the study area. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **87** Suppl 2, 19–23.
- Muirhead-Thomson, R.C. (1945) Studies on the breeding places and control of *Anopheles gambiae* and *A. gambiae* var. *melas* in coastal districts of Sierra Leone. *Bulletin of Entomological Research* **36**, 185–252.
- Ribbands, M.C.R. (1944a) Differences between *Anopheles melas* and *Anopheles gambiae*. II. Salinity relations of larvae and

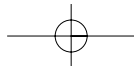




- maxillary palp banding of adult females. *Annals of Tropical Medicine and Parasitology* **38**, 87–99.
- Ribbands, M.C.R.** (1944b) The influence of rainfall, tides and periodic fluctuations on a population of *Anopheles melas*, Theo. *Bulletin of Entomological Research* **35**, 271–295.
- Scott, J.A., 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.
- Sylla, M., Stein, A., van Breemen, N. & Fresco, L.O.** (1995) Spatial variability of soil salinity at different scales in the mangrove rice agro-ecosystem in West Africa. *Agriculture, Ecosystems and Environment* **54**, 1–15.
- Thomas, C.J. & Lindsay, S.W.** (2000) Local-scale variation in malaria infection amongst rural Gambian children estimated by satellite remote sensing. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **94**, 159–163.
- Thomson, M., Connor, S., Bennett, S., D'Alessandro, U., Milligan, P., Aikins, M., Langerock, P., Jawara, M. & Greenwood, B.** (1996) Geographical perspectives on bed net use and malaria transmission in The Gambia, West Africa. *Social Science and Medicine* **43**, 101–112.
- Toure, Y.T., Traore, S.F., Sankare, O., Sow, M.Y., Coulibaly, A., Esposito, F. & Petrarca, V.** (1996) Perennial transmission of malaria by the *Anopheles gambiae* complex in a North Sudan savannah area of Mali. *Medical and Veterinary Entomology* **10**, 197–199.
- Trolldalen, J.M.** (1991) *On the fringe: a systems approach to the evolution of the environment and agricultural production in The Gambia, West Africa 1948–1983*. NORAGRIC Occasional Series C. Development and environment: 10.
- Vercruyse, J.** (1985) Entomological study on the transmission of human malaria in the Senegal River Basin (Senegal). *Annales de la Société Belge Médecine Tropicale* **65** Suppl. 2, 171–179.

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