



Mapping the ranges and relative abundance of the two principal African malaria vectors, *Anopheles gambiae sensu stricto* and *An. arabiensis*, using climate data

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Members of the *Anopheles gambiae* complex are major malaria vectors in Africa. We tested the hypothesis that the range and relative abundance of the two major vectors in the complex, *An. gambiae sensu stricto* and *An. arabiensis*, could be defined by climate. Climate was characterized at mosquito survey sites by extracting data for each location from climate surfaces using a Geographical Information System. Annual precipitation, together with annual and wet season temperature, defined the ranges of both vectors and were used to map suitable climate zones. Using data from West Africa, we found that where the species were sympatric, *An. gambiae s.s.* predominated in saturated environments, and *An. arabiensis* was more common in sites subject to desiccation ($r^2=0.875$, $p<0.001$). We used the nonlinear equation that best described this relationship to map habitat suitability across Africa. This simple model predicted accurately the relative abundance of both vectors in Tanzania ($r_s=0.745$, $p=0.002$), where species composition is highly variable. The combined maps of species' range and relative abundance showed very good agreement with published maps. This technique represents a new approach to mapping the distribution of malaria vectors over large areas and may facilitate species-specific vector control activities.

Keywords: Africa; *Anopheles arabiensis*; *Anopheles gambiae*; climate surfaces; geographical information systems; malaria

1. INTRODUCTION

Malaria is the most common and devastating disease in the tropics (WHO 1993a) and the situation is getting worse (WHO 1993b). Eighty per cent of all cases occur in sub-Saharan Africa, accounting for 250–450 million clinical cases and over one million deaths each year. Here, malaria parasites are transmitted largely by mosquitoes of the *Anopheles gambiae* complex, which is the most efficient vector system in the world. This complex consists of a number of mosquito species that vary in their ability to transmit falciparum malaria in Africa (White 1974; Coluzzi *et al.* 1979; Coluzzi 1984, 1992). The two principal vectors in the complex are *An. gambiae sensu stricto*, which is the most efficient vector, and *An. arabiensis*.

There are enormous technical and operational difficulties in producing a high-resolution map of these vectors across the 42 560 000 km² land surface of Africa. One limitation is that complex laboratory techniques are required to distinguish these morphologically similar species, e.g. using analysis of polytene chromosome banding patterns (Hunt 1973), allozyme analysis (Miles 1978), high performance liquid chromatography of cuticular hydrocarbons (Carlson & Service 1980) and molecular methods (Collins *et al.* 1987; Hill & Crampton 1994). Distribution maps of these vectors have been

published for individual countries and collated as atlases (Davidson & Lane 1981 (figures redrawn and cited by White (1985)); White 1989). These are based on the presence of the two mosquito species found at different sites. This information is displayed either as points on a map where the specimens were collected (Davidson & Lane 1981 (figures redrawn and cited by White (1985))) or summarized as a range map, by interpolating between these points (White 1989). However, such maps suffer two major deficiencies. First, experts inevitably have to use their judgement, based upon sparse data, to interpolate distribution patterns, often over extensive areas. Second, the maps show past distribution patterns, and it is difficult to make adjustments for recent environmental changes in an area. Over the past two decades new approaches have been developed for mapping the distribution of mosquitoes over large areas. Floral composition and vegetation structure has been used to identify breeding sites of rural mosquitoes (Gabinaud 1987). Remote sensing from aircraft or earth-orbiting satellites has also been used to identify potential wetland breeding sites of mosquitoes (Wagner *et al.* 1979; Linthicum *et al.* 1987; Wood *et al.* 1992; Pope *et al.* 1994) as well as adult mosquito numbers (Rejmankova *et al.*, 1995; Roberts *et al.* 1996; Thomson *et al.* 1996).

Many studies have shown that climate is a major factor governing the distribution of insects (Andrewartha & Birch 1954; Sutherst *et al.* 1995), either by acting directly

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on insect populations themselves or indirectly by affecting the structure of the ecosystem they inhabit. Moreover, because *An. gambiae s.s.* is known to prefer more humid areas and *An. arabiensis* is more common in arid ones, we hypothesized that the species ranges and relative proportions of both vectors where they were sympatric could be defined using climatological criteria.

2. MATERIAL AND METHODS

We used a spatial environmental database for Africa (Data Exploration Tool (DET) (Corbett *et al.* 1996)), operating within a geographical information system (GIS, Arc/Info (ESRI 1996)), to describe the climate at sites where mosquito surveys had been carried out in the past. DET contains a set of continuous surfaces, at a three arc-minute resolution, describing climate, topography, human population density and soil water holding capacity. Climate surfaces were produced by Corbett & Kruska (Corbett & Kruska 1994; Corbett 1995) from coefficients calculated by Hutchinson *et al.* (1995) using data collected from meteorological stations.

(a) *Characterizing species' ranges*

Published maps (approximately 1:50 000 000) showing the presence of both vectors (Davidson & Lane 1981 (figures redrawn and cited by White (1985)) were converted into a digital format by scanning the maps at 300 d.p.i. The images were then registered and rectified to real world co-ordinates using image integration tools in the GIS. Registration errors for locations were well below the resolution required for grid coverages. The published maps recorded the presence of mosquitoes on a one-degree-square grid. As climate coverages from DET were described at a finer resolution of three arc-minutes, climate coverages were aggregated to obtain mean values for each one-degree square using the GIS. The following coverages were aggregated: (i) the number of consecutive months in the main wet season (defined by precipitation/potential evapotranspiration ($P/PE \geq 0.5$)); (ii) the number of consecutive months in the main dry season (defined by $P/PE < 0.5$); (iii) the number of consecutive months in the minor wet season (where present); (iv) the number of consecutive months in the minor dry season (where present); (v) total annual precipitation; (vi) total annual evapotranspiration; (vii) maximum annual temperature; (viii) minimum annual temperature; (ix) mean minimum annual temperature; (x) mean P/PE in the five consecutive months of greatest mean P/PE ; (xi) mean maximum temperature of this period; and (xii) mean minimum temperature of this period.

We defined spatial ranges based upon minimum and maximum climate values observed at sites where each species was present and selected the minimum number of variables that excluded all unsuitable cells.

(b) *Characterizing relative abundance*

The location and relative proportion of *An. gambiae s.s.* and *An. arabiensis* collected at individual sites was determined from maps showing the distribution of the *An. gambiae* complex in Guinea Bissau (approximate scale 1:2 400 000 (Petrarca *et al.* 1983)), Nigeria and Niger (approximate scale 1:6 250 000 (Coluzzi *et al.* 1979)) and the Senegambia (approximate scale 1:2 800 000 (Bryan *et al.* 1987) and 1:4 500 000 (Petrarca *et al.* 1987)). The abundance of mosquitoes at each site was not reported. Because the data on relative abundance were displayed as maps, the reference co-ordinates of each site was determined by overlaying

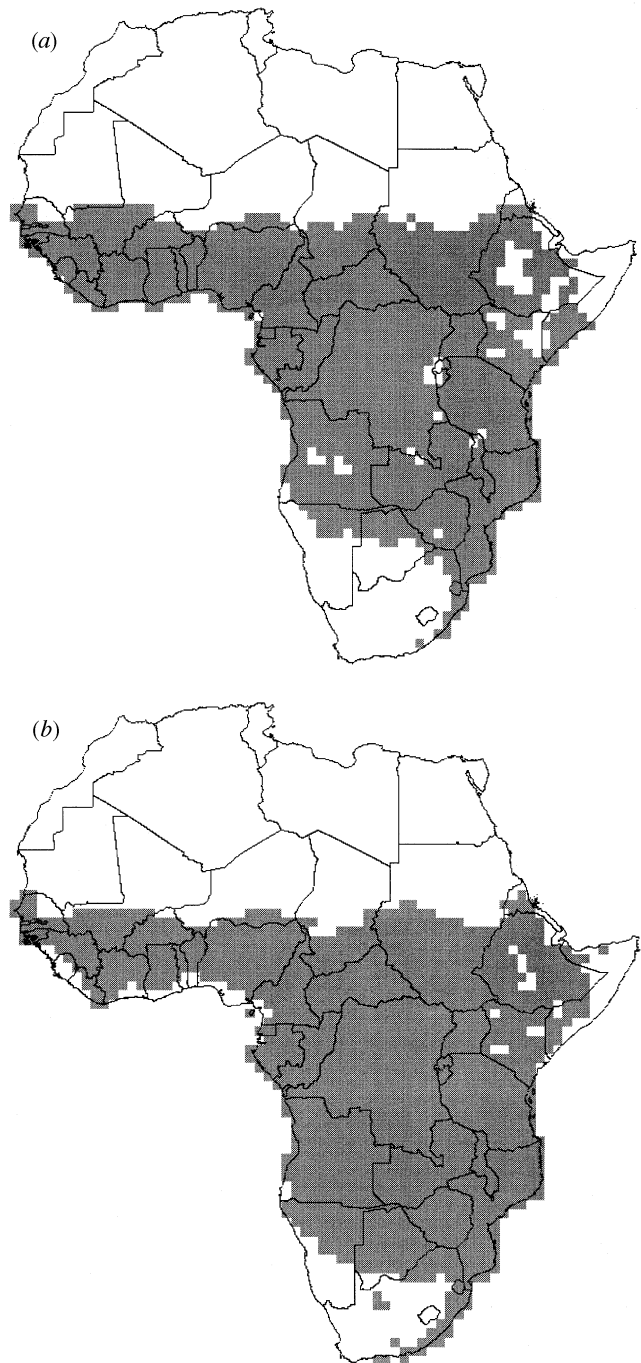


Figure 1. Climate suitability zone for (a) *An. gambiae s.s.* and (b) *An. arabiensis*.

scanned digitized versions of these maps on 1:1 000 000 scale digital maps of West Africa (Mundocart 1991) or East Africa (DET; Corbett *et al.* 1996). National boundaries, coastlines, lakes and rivers were used to link survey maps with true world co-ordinates using Arc/Info geo-rectification tools.

Descriptions of the climate at each survey site were obtained by querying climate surfaces within DET. At each site we obtained values describing annual precipitation, five-month optimum values for precipitation, mean monthly maximum and minimum temperatures, potential evapotranspiration and maximum and minimum temperature, population density and soil water capacity. In our analysis, we selected a five-month period of precipitation in preference to annual rainfall, as malaria transmission in much of West Africa is seasonal rather than perennial.

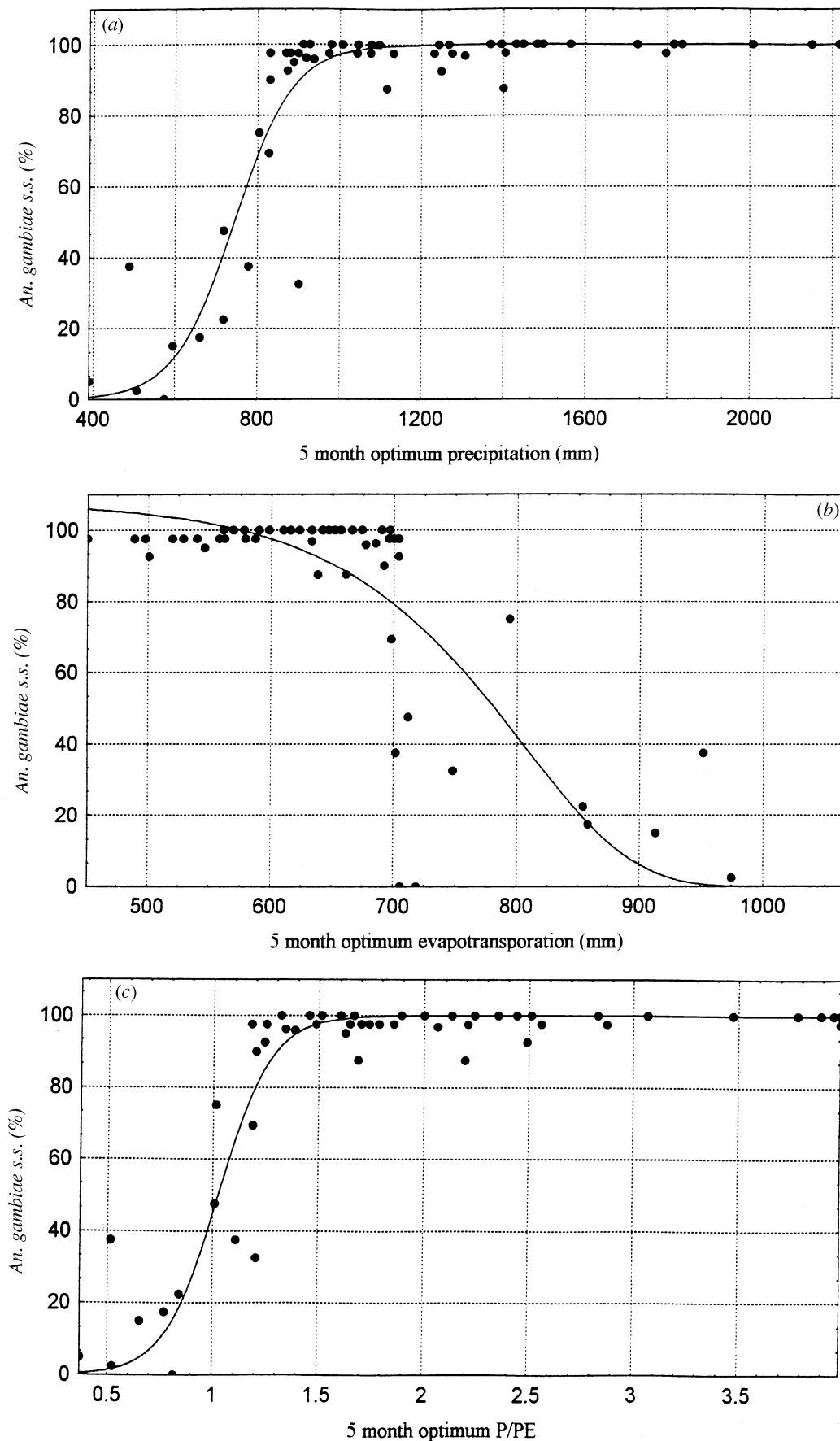


Figure 2. Relationship between the relative abundance of *An. gambiae* s.s. and *An. arabiensis* in individual villages (*V*) and (a) five-monthly maximum precipitation (*P*), (b) five-monthly evapotranspiration (*PE*) and (c) the index P/PE .

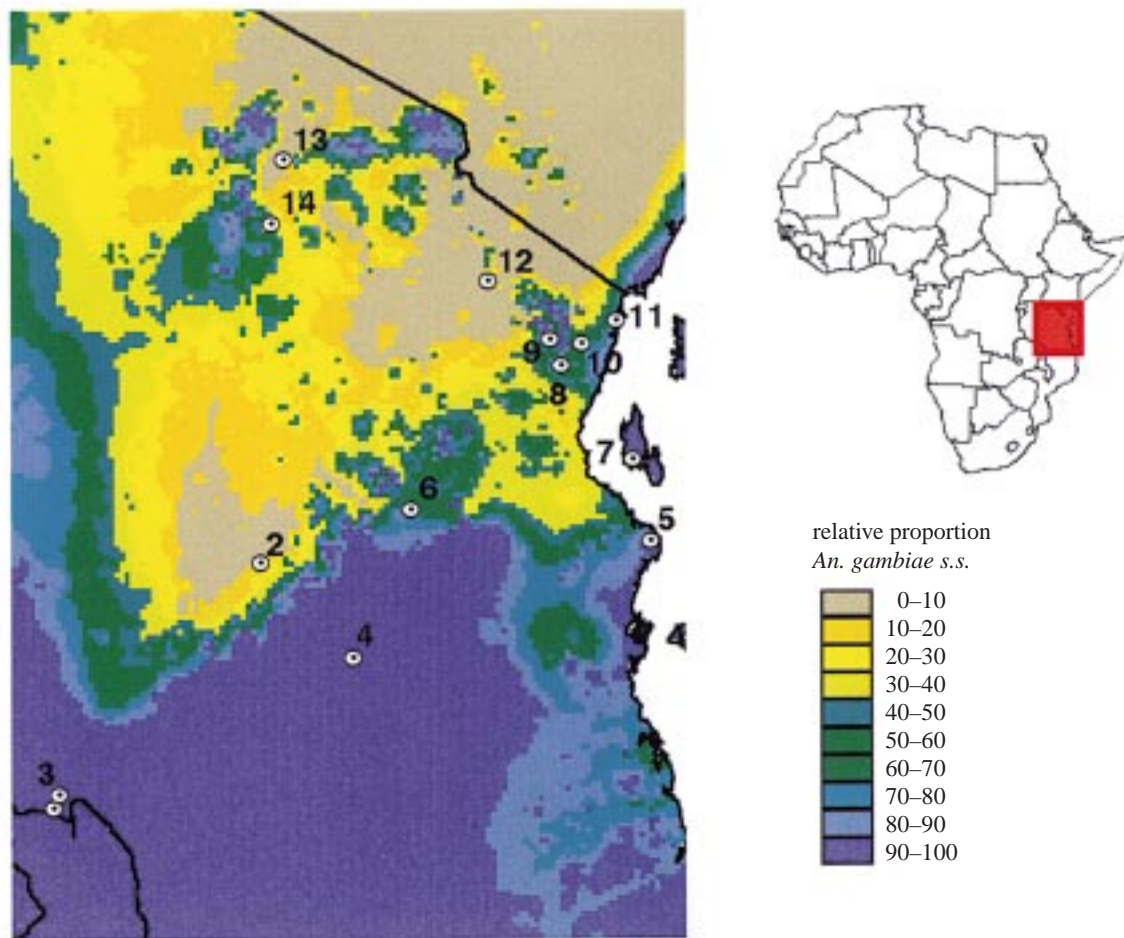


Figure 3. Expected distributions of the relative proportion of *An. gambiae s.s.* in Tanzania.

Relationships between species composition and environmental determinants were described using nonlinear regression techniques. The equation representing the line of best fit was used to create a three-arc-minute grid surface of potential relative abundance of *An. gambiae s.s.* and *An. arabiensis* within Arcinfo.

(c) Model validation

The predicted range maps of both vector species were compared with published maps (approximate scales 1:50 000 000 (Davidson & Lane 1981 (figures redrawn and cited in White (1985))) and 1:125 000 000 (White 1989)). The map of relative abundance was compared with field data from Tanzania (approximate scale 1:5 000 000 (Mnzava & Kilama 1986)). At each site where mosquitoes surveys had previously been carried out we used the GIS to extract the expected proportion of *An. gambiae s.s.* and *An. arabiensis* from the potential relative abundance surface. Comparisons between observed and expected values were made using Spearman's rank correlation.

3. RESULTS

(a) Vector ranges

The climate suitability zone that best described the range of *An. gambiae s.s.* lay within areas with total annual precipitation 330–3224 mm, maximum annual temperature 25–42 °C, minimum annual temperature 5–22 °C, mean

maximum temperature of the wet season 25–38 °C and mean minimum temperature of the wet season 11–24 °C. For *An. arabiensis* the climate suitability zone was defined as lying within areas with total annual precipitation 237–415 mm, maximum annual temperature 22–41 °C, minimum annual temperature 2–21 °C, mean maximum temperature of the wet season 21–37 °C and mean minimum temperature of the wet season 11–24 °C. These zones are shown in figure 1a,b.

(b) Relative abundance

The proportion of *An. gambiae s.s.* and *An. arabiensis* in individual villages (V) was correlated with both five-month optimum precipitation (P , where $V=100/[1+(30\,000)\exp(-0.01387P)]$; $r^2=0.872$, $n=64$, $p<0.001$) and potential evapotranspiration (PE , where $V=108.05\exp\{-0.0111\exp[0.0111(PE-400)]\}$, $r^2=0.629$, $n=64$, $p<0.001$) through simple nonlinear equations (figure 2a,b). Five-month precipitation totals were similar to annual values at each site ($r^2=0.891$, $n=64$, $p<0.001$). No significant correlations were found with temperature, population density, or soil moisture.

Our analysis of the 74 survey sites followed a hierarchical approach, where climate was a first-order determinant of ecological structure at a continental scale. We assumed that at the spatial grain of individual sampling sites some local factors also needed to be considered. Thus, four sites

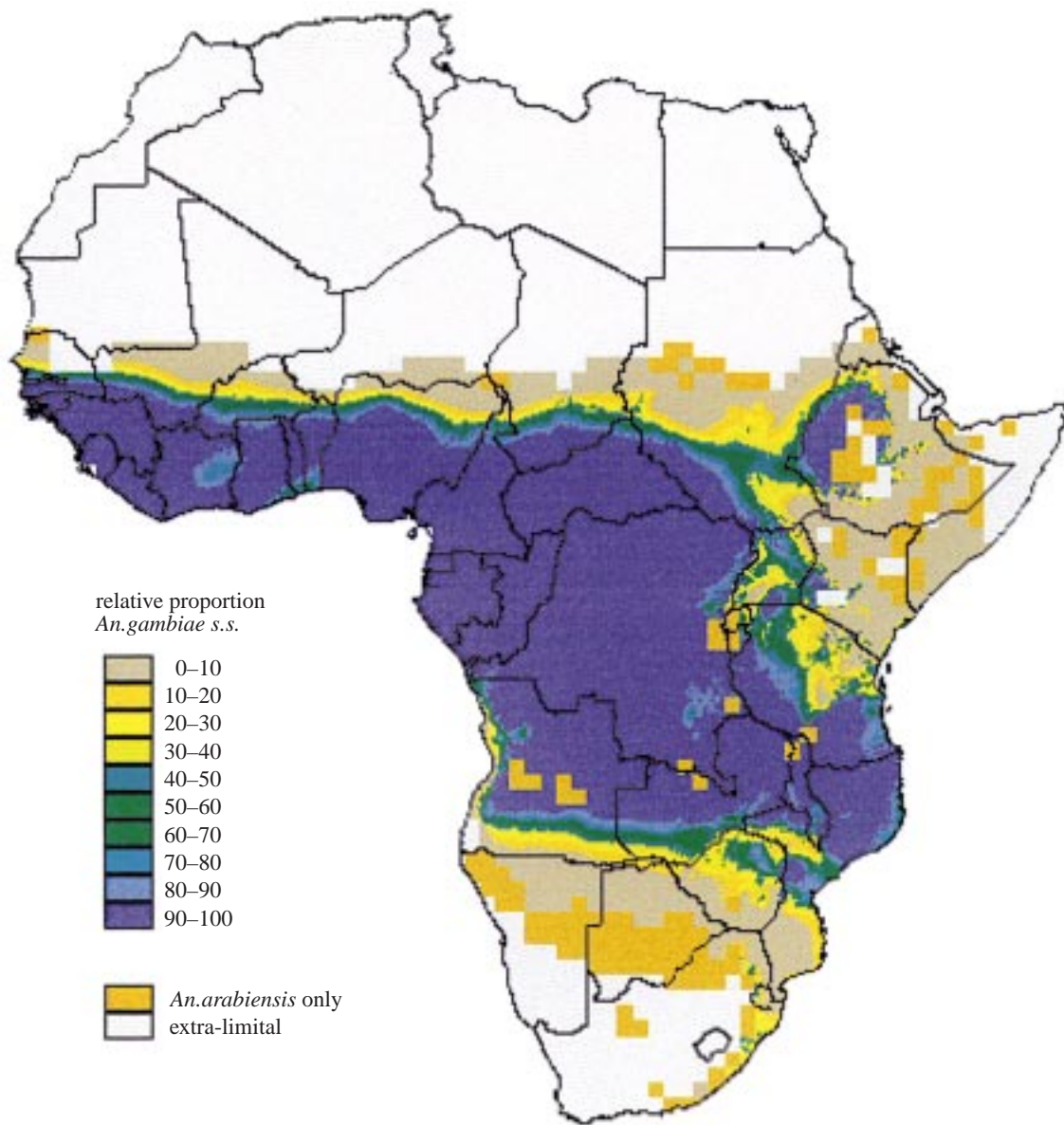


Figure 4. Expected distributions (three-arc-minute grid cells) of the relative proportion of *An. gambiae s.s.* and *An. arabiensis* in Africa within the limits of the climate suitability zone of *An. gambiae s.s.* (from figure 1a). The distribution of *An. arabiensis* lying outside this zone is also shown in one-degree grid cells (from figure 1b).

in areas of high population density (more than 200 people per square kilometre, derived from DET) with unusually high proportions of *An. arabiensis* in southern Nigeria were excluded from the analysis as *An. arabiensis* is better adapted to urban environments in West Africa than *An. gambiae s.s.* (Coluzzi *et al.* 1979; Chinery 1984; Petrarca *et al.* 1986; Trape *et al.* 1992). A further six sites along the Senegal River Valley in northern Senegal were also excluded as local climatic effects associated with major water bodies and irrigated areas in arid zones would make it a more favourable environment for this humid-loving species.

We used the ratio of precipitation to potential evapotranspiration to produce an index of saturation deficit (i.e. five-month optimum P/PE), and found that this index best explained the distribution of the two vectors (where $V=100/[(1+3586.98) \exp(-7.9918(P/PE))]$,

$r^2=0.875$, $n=64$, $p<0.001$; figure 2c). Here the relative abundance of both vectors pivots around the value of 1.0 (a ratio of $P/PE=1.02$ corresponds to 50% *An. gambiae s.s.* or *An. arabiensis*). Thus, at values of $P/PE>1.0$, where precipitation exceeds potential evapotranspiration, the climate is moist, and *An. gambiae s.s.* predominates. When $P/PE<1.0$, organisms have to contend with problems of water loss, and *An. arabiensis* is more common.

(c) **Model validation**

The climate variables that best described the range of both vectors were used to generate distribution maps within DET. These maps corresponded well with the known distribution of these mosquitoes in Africa (Davidson & Lane 1981, cited in White (1985)); White 1989). The equation that best described the relationship between the P/PE ratio and relative species abundance

Table 1. *Observed and expected distributions of the relative proportion of An. gambiae s.s. in Tanzania*

site	<i>An. gambiae s.s.</i> (%)	
	expected	observed
1	100	100
2	12	0
3	100	100
4	100	94
5	92	100
6	76	100
7	96	83
8	77	87
9	70	88
10	69	91
11	80	91
12	1	6
13	7	0
14	37	0

(see figure 2c) was used within the GIS to map the estimated proportion of *An. gambiae s.s.* and *An. arabiensis* within three-arc-minute cells within the previously calculated range of *An. gambiae s.s.* (figure 3). The accuracy of this model, developed using data from West Africa, was validated by comparing the relative proportion of each species collected at field sites in East Africa (Mnzava & Kilama 1986) with expected values computed for *P/PE* (table 1). There was a significant correlation between observed and expected values ($r_s=0.745$, $n=14$, $p=0.002$). Finally, the coverages of species' ranges and relative abundance of *An. gambiae s.s.* and *An. arabiensis* in Africa within the limits of the climate suitability zone of *An. gambiae s.s.* were combined to illustrate the relative abundance and distribution of these two important species across Africa (figure 4).

4. DISCUSSION

We used climate surfaces to examine the relationship between climate and the distribution of two important African malaria vectors, *An. gambiae s.s.* and *An. arabiensis*. These surfaces are based on data derived from 621 meteorological stations and are produced by interpolating between these points (Hutchinson & Corbett 1995). Using data extracted from these surfaces we have shown that the range and relative abundance of *An. gambiae s.s.* and *An. arabiensis* are correlated with climate at a regional scale.

Most importantly, we found that relative abundance of these species was related to an index of saturation (i.e. five-monthly maximum precipitation/five-monthly maximum potential evapotranspiration). Where this ratio exceeded a value of 1.0 and the air was moist, *An. gambiae s.s.* predominated, whereas in areas where this value was below 1.0, the air was dry and *An. arabiensis* was more common. Although this relationship has never been formally elucidated until now, our finding concurs with the known biology of *An. arabiensis*, which has a number of strategies that allow it to persist in arid conditions. Adult females will lay their eggs on damp surfaces, rather than water, with hatching being delayed in a

proportion of eggs (Coluzzi 1965). Females will also aestivate during periods of prolonged dryness (Omer & Cloudsley-Thompson 1968; Omer 1970), and dry season refugia exist in which *An. arabiensis* thrive and rapidly colonize other areas at the start of the rainy season (White 1974). However, there may be other, as yet unidentified mechanisms that allow this species to survive in dry environments.

The simple nonlinear model used to describe relative abundance was derived from survey data collected in West Africa (Bryan *et al.* 1987; Coluzzi *et al.* 1979; Petrarca *et al.* 1983, 1987). We used this equation to generate a map of relative abundance for the whole of Africa and tested our map against field data from Tanzania, East Africa. We found an excellent agreement between the observed and expected values, and were able to discriminate between sites where *An. gambiae s.s.* and *An. arabiensis* predominated with 100% consistency. This result suggests that the climatic factors governing the distribution of the vectors are the same in West Africa as in East Africa: a distance from coast-to-coast of about 6400 km. Such a strong correlation is surprising considering the large variation in species composition which can occur at different times of the year (White 1974; White *et al.* 1972; Di Deco *et al.* 1981), as well as between years (Faye *et al.* 1997). Moreover, the climate surfaces used in this analysis are long-term averages and are not necessarily contemporaneous with the years when the surveys were conducted. Nonetheless, there was good agreement between the predicted and observed relative abundance of *An. gambiae s.s.* and *An. arabiensis* across most of Africa (Davidson & Lane 1981 (cited in White (1985)); White 1989).

Our findings may be of relevance to control programmes as we identify different patterns of malaria transmission in areas where field data is not available. Thus vector-control activities targeted at *An. arabiensis* need to consider the exophilic (tending to rest outdoors) and zoophagic (tending to feed on animals other than humans) habits of this species. In such areas, indoor spraying with residual insecticides is likely to be less successful because of the exophilic habits of the vector.

As we have shown that these species distributions are intimately linked to precipitation and potential evapotranspiration, changes in rainfall may lead to changes in transmission patterns. Sub-Saharan Africa is experiencing a prolonged drought, with a 21% decrease in annual rainfall over the past 100 years (Hulme 1996). Consequently, *An. arabiensis* is likely to replace *An. gambiae s.s.* as long as the drought continues. Our model could be used to explore these changing patterns associated with different climate change scenarios. Importantly, the ratio of precipitation to potential evapotranspiration is likely to be a better measure of transmission risk than rainfall alone when modelling the risk of malaria transmission in Africa.

We have produced and tested a model for predicting the range and relative abundance of two important vectors of malaria in Africa at a regional and a continental scale. This is a first-order model as it is based on climate and operates at a coarse spatial resolution. Further studies are required at a finer resolution to improve predictions at a local scale. This technique of using climate surfaces offers promise as a rapid technique for mapping the distribution of disease vectors in different parts of the world.

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