The Effects of Climatic Factors on the Distribution and Abundance of Malaria Vectors in Kenya

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ABSTRACT Since 1988 malaria epidemics have occurred in multiple sites in western Kenya highlands. Climatic variability has been associated with some of the recent epidemics. We examined influences of climatic factors on the distribution and abundance of three malaria vector species, *Anopheles gambiae*, *Anopheles arabiensis*, and *Anopheles funestus* in western Kenya and in the Great Rift Valley. Mosquito samples were collected from the lowland and highland areas with various climatic conditions. The three vector species were abundant in the lower part of western Kenya. *An. arabiensis* was not found in the areas above 1,400 m elevation in western Kenya. Although *An. gambiae* and *An. funestus* were found in the sites above 1,700 m in western Kenya, their densities were <1 per house. In the Great Rift Valley, *An. gambiae* was not recorded. *An. funestus* was more widely distributed than the other two species. A stepwise multiple regression analysis found that moisture index was the most important variable in shaping species composition of the *An. gambiae* complex. Relative abundance of *An. gambiae* was positively associated with moisture index, suggesting that *An. gambiae* is more adapted to moist climate. Seasonal differences in species composition were significant in western Kenya, and the proportion of *An. funestus* was higher in the dry season than the rainy season. Influence of temperature on vector density was significant for all three species. These results imply that climate changes alter the distribution and abundance of malaria vectors in future.

KEY WORDS *Anopheles gambiae*, *Anopheles arabiensis*, *Anopheles funestus*, Kenya, Great Rift Valley, malaria

IN AFRICA, THE most virulent malaria parasite, *Plasmodium falciparum*, is transmitted primarily by the *Anopheles gambiae* Giles complex and *Anopheles funestus* Giles. The *An. gambiae* complex is a group of closely related, morphologically indistinguishable species. Two or more species within the species complex coexist in many areas (Coetzee et al. 2000). Because individual species differ in host-biting preference, abundance, and vector competence (Highton et al. 1979, Petrarca et al. 1991), identifying the mosquito vectors to species level and determining species distribution patterns in heterogeneous environments are critical for malaria vector control.

Climatic factors such as precipitation and temperature are important determinants of the range and relative abundance of individual species of the *An. gambiae* complex (Lindsay et al. 1998). *An. gambiae* Giles is usually the predominant species in saturated environments, but *Anopheles arabiensis* Patton is more common in arid areas (Coetzee et al. 2000). Distribution of *An. funestus*, however, is strongly affected by the availability of permanent waters (Ingram and De Meillon 1927, Evans 1938). Climatic conditions are directly associated with elevation. Temperature decreases as elevation increases, and consequently the abundance and species compositions of malaria vectors may change with elevation. For example, vector density is much lower in Ugandan highlands than in low-elevation areas (Lindblade et al. 2000a). Studies by Shililu et al. (1998) with limited sampling sites in western Kenya found no *An. arabiensis* in areas with elevation around 1,500 m above sea level (a.s.l.), whereas *An. arabiensis* is abundant in the basin of Lake Victoria with elevation <1,300 m a.s.l.

In East African highlands, sporadic malaria outbreaks occurred from the 1920s to the 1950s (Garnham 1948, Roberts 1964). Since 1988, malaria epidemics have occurred nearly every year and are a major public health threat in western Kenya highlands (Malakooti et al. 1998). Unlike the people who live in malaria-endemic areas, the highland populations generally lack immunity against malaria and are particularly vulnerable to malaria. Several hypotheses have been proposed to explain increased highland malaria transmission, including land use changes, cli-

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mate changes, drug resistance, cessation of malaria control activities, and demographic changes (Lindsay and Martens 1998; Malakooti et al. 1998; Mouchet et al. 1998; Lindblade et al. 2000b; Githeko and Ndegwa 2001). However, Hay et al. (2002) found that temperature, rainfall, and the number of months suitable for *P. falciparum* transmission have not changed significantly during the past century in four East African highland sites, suggesting that no regional climate change has occurred in East Africa highlands.

In Kenya, 80% of the 27 million people live in the western and central provinces, and about one-third of the population live in highlands. However, vector research has primarily focused on low-elevation, malaria-endemic areas, and information on malaria vector biology in highlands is limited. Studies on malaria vector species distribution and its relationship with climatic factors and elevation provide valuable information on malaria transmission in African highlands. In this paper, we report the results of three cross-sectional surveys on malaria vectors from low-altitude to high-altitude sites with various climatic conditions in western Kenya and the Great Rift Valley.

Materials and Methods

Study area and mosquito sampling. Adult anopheline mosquitoes were collected in three cross sections (Fig. 1). The first cross section was along the Yala River. Nineteen sites were sampled in the river region, and the elevation of the sampling sites ranged from 1,150 m to 2,020 m a.s.l. The second cross section included eight sampling sites along the Nyando River. The elevation of the sampling sites ranged from 1,155 m to 1,770 m a.s.l. Yala and Nyando Rivers originate from high-altitude hills (elevation, 1,900–2,800 m a.s.l.) on the west side of the Great Rift Valley and drain into Lake Victoria at 1,140 m a.s.l. The third cross section was between Lake Naivasha and Lake Baringo in the Great Rift Valley, where eight sites were sampled for adult mosquitoes. The elevation of the valley sites ranged from 910 m to 1,900 m a.s.l.

Anopheline mosquitoes were collected from 5 to 15 houses at each site in May 2000 during the peak of the long rainy season. Each site was sampled once during the period. Because mosquito abundance may vary between dry and rainy seasons, the sites in the Yala River region were also sampled July 6–9, 2000, during the dry period. All houses were constructed with mud and thatch. The sampled houses in western Kenya were situated closest to the main bridge along major roads in each site. In the Great Rift Valley, the houses were situated closest to the valley bottom in each site. Coordinates of each house were recorded using a hand-held GPS unit. Indoor resting mosquitoes were sampled from 700 to 1100 hours using the pyrethrum spray catch method (World Health Organization 1975), and the collections were preserved in 95% ethanol for subsequent species identification.

Species identification. All female mosquitoes were examined microscopically to distinguish the *An. gambiae* species complex from *An. funestus*, based on the identification keys of Gillies and Coetzee (1987). Because female anopheline mosquitoes are directly responsible for malaria transmission, and the majority of specimens collected using in-door pyrethrum spray method were females, the analyses focused on female anopheline mosquitoes only. Individual species within the *An. gambiae* species complex were identified using the rDNA - polymerase chain reaction (PCR) method (Scott et al. 1993). If the initial PCR testing failed to amplify a sample, then the PCR analysis was repeated once or twice until successful amplification was achieved. If a sample could not be identified after three PCR amplifications, it was scored as unknown (Minakawa et al. 1999). The unidentified specimens were probably poorly preserved or morphologically misidentified as members of the *An. gambiae* complex.

Data analyses. (a) Species composition of anopheline mosquitoes. chi-square tests were used to determine whether anopheline species composition varied between the rainy and dry seasons for the sites along the Yala River. To determine the effects of climatic variables on the relative abundance of *An. gambiae* during the rainy season, we used stepwise multiple regression analysis with the proportion of *An. gambiae* in the *An. gambiae* species complex as dependent variable. Stepwise regression analysis was used to identify important variables while minimizing the effect of collinearity among the climatic variables. The initial model included annual mean maximum temperature, mean minimum temperature and mean moisture index as independent variables. The temperature, rainfall, and evapotranspiration data were obtained from the ACT database with a spatial resolution of 0.05^0 (Corbett et al. 2000), and average values from 1961 to 1990 were used. Moisture index was calculated as the ratio of precipitation to potential evapotranspiration. The elevations of the sites were not included in the model because of close association between climatic factors and elevation. The relative abundance of *An. gambiae* was arcsine transformed, and the three independent variables were log transformed.

(b) Anopheline mosquito abundance. Paired *t*-tests were used to determine differences between rainy and dry seasons in absolute density of each anopheline species for the sites along the Yala River. To determine the relationship between anopheline mosquito densities and climatic factors, stepwise multiple regression analysis described above was conducted. Dependent variables were the absolute densities of *An. gambiae*, *An. arabiensis*, and *An. funestus* mosquitoes. Mosquito densities were log transformed.

Results

Anopheline species distribution. Among the 35 sites sampled from the three cross sections, anopheline mosquitoes were found from 28 sites; they were not found in five sites in the Great Rift Valley and two sites in the upper Yala River region (Fig. 1). Three species of malaria vectors (*An. gambiae*, *An. arabiensis*, and *An. funestus*) were found in the Yala River and the Nyando River regions, whereas *An. gambiae* was absent from

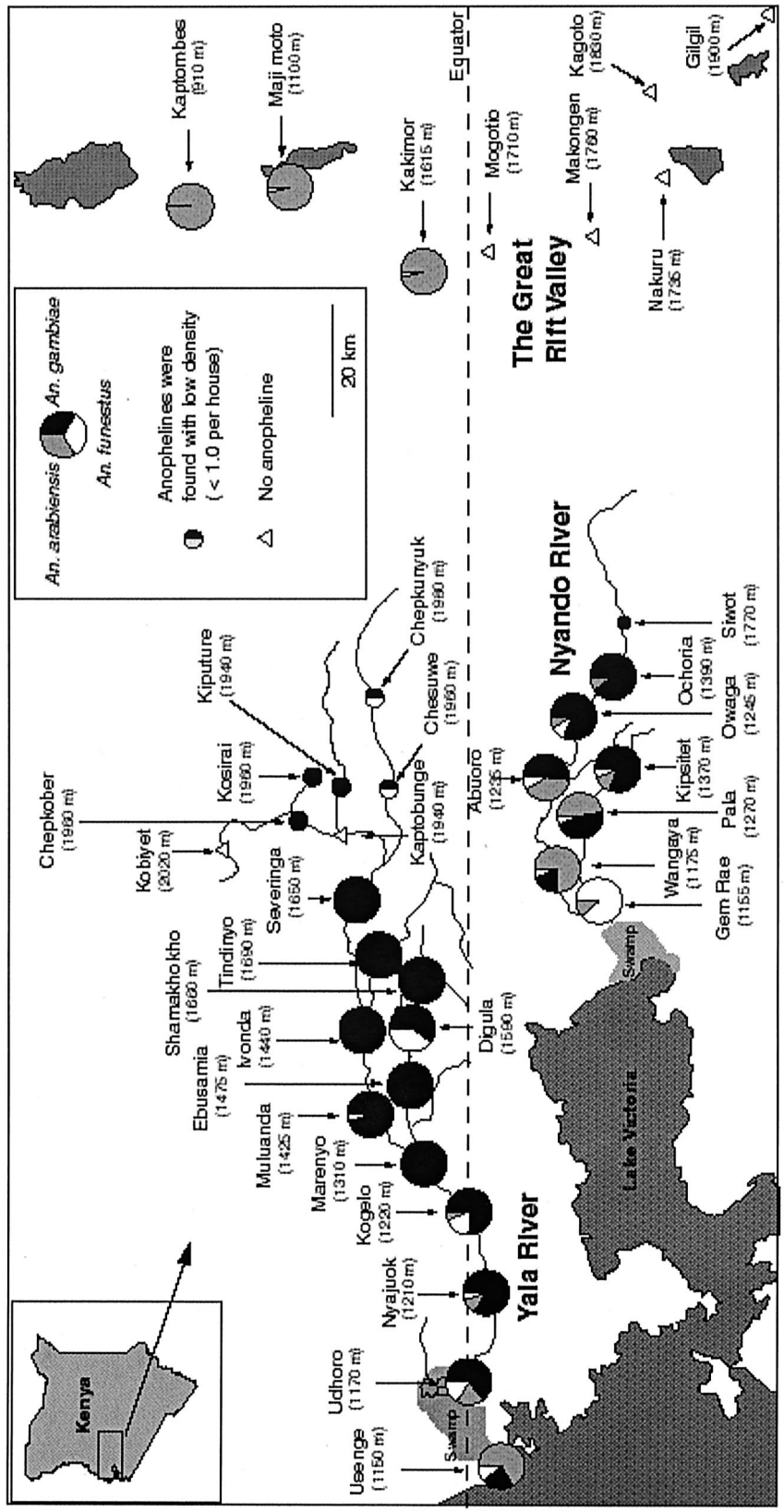

Fig. 1. Map of the study area. The map shows the sampling sites, elevation, and anopheline mosquito species composition during the rainy season in the Great Rift Valley and western Kenya.

Table 1. Total number anopheline mosquitoes collected in Yala River and Nyando River regions and the Great Rift Valley in Kenya

Season	Areas	*An. gambiae*		*An. arabiensis*		*An. funestus*		Unidentified
		No. (%)	Density[a] (SE)	No. (%)	Density[a] (SE)	No. (%)	Density[a] (SE)	No. (%)
Rainy period	Yala River	609 (73.6)	6.4 (1.4)	126 (15.2)	1.3 (0.5)	90 (10.9)	1.0 (0.3)	3 (0.4)
Dry period	Yala River	133 (51.8)	1.4 (0.3)	17 (6.5)	0.2 (0.1)	104 (40.5)	1.1 (0.3)	3 (1.2)
Rainy period	Nyando River	573 (38.6)	12.7 (2.7)	380 (25.6)	8.5 (1.6)	504 (33.9)	11.2 (4.5)	28 (1.9)
Rainy period	Great Rift Valley	None	None	660 (96.9)	13.2 (3.8)	10 (1.5)	0.2 (0.1)	11 (1.6)

[a] Density is defined as the number of mosquitoes per house.

the Great Rift Valley (Fig. 1). In the Yala River region, *An. gambiae* was found in 17 sites including 5 sites >1,900 m a.s.l., and *An. arabiensis* in only four sites of elevation <1,300 m a.s.l. during both rainy and dry seasons. *An. funestus* were observed from the sites <1,600 m a.s.l., but it was also recorded in two sites >1,900 m elevation. In the Nyando River region, all three species were found in sites <1,400 m a.s.l., and one site >1,700 m a.s.l. had only *An. gambiae* (Fig. 1). *An. arabiensis* were found at three sites and *An. funestus* in two sites in the Great Rift Valley, but no anopheline mosquitoes were collected in the sites >1,700 m a.s.l. (Fig. 1).

Anopheline mosquito abundance. In total, 3,251 anopheline females were collected from 28 sites, and 3,206 (98.6%) were identified to species. In the Yala River region, more than 70% of the anopheline adults were *An. gambiae* during the rainy season, and the proportions of *An. arabiensis* and *An. funestus* were 15.1% and 10.8%, respectively (Table 1). During the dry season, the proportion of *An. gambiae* was reduced to 51.8% and that of *An. funestus* increased to 40.5%, and the species composition between the rainy and dry seasons was significantly different ($\chi^2 = 273.0$, df = 1, $P < 0.01$). *An. arabiensis* and *An. funestus* dominated in the lower regions of the Yala and Nyando Rivers. In the Great Rift Valley, 96.9% of the collected mosquitoes were *An. arabiensis*, and 1.5% were *An. funestus* (Table 1).

Anopheline mosquito densities, expressed as the number of female adults per house, generally declined with increased elevation in western Kenya except for *An. gambiae* in the Yala River region during the dry season and in the Nyando River region during the rainy season (Fig. 2). For example, *An. arabiensis* and *An. funestus* densities were 12.6 and 10.4 mosquitoes per house in sites near the swamps in the mouths of Yala River (1,170 m a.s.l.) during the rainy season, however, their densities were reduced to <1 mosquito per house in sites >1,700 m a.s.l. Although *An. gambiae* densities were significantly lower during the dry season than during the rainy season ($t = 2.30$, df = 1, $P < 0.05$; Fig. 2A and 2B), the negative correlation between elevation and mosquito densities also holds for the dry season. Similar relationship between elevation and *An. gambiae* and *An. arabiensis* densities was observed in the Nyando River region and the Great Rift Valley (Fig. 2C and 2D).

Relationship between climatic factors and anopheline mosquito species compositions and densities. Using stepwise multiple regression analysis with the proportion of *An. gambiae* in the *An. gambiae* species complex as dependent variable, we found that moisture index was the only variable significantly associated with *An. gambiae* relative abundance (Table 2). The relationship between moisture index and *An. gambiae* species composition is shown in Fig. 3. No *An. gambiae* populations were found in sites with moisture index <0.7. The percentage of *An. gambiae* increased rapidly with slight increases in moisture index when it was >0.7 (Fig. 3). Moisture index does not linearly correlate with elevation in the three regions, although it is much lower for sites in the Great Rift Valley than those of same elevation in western Kenya regions (Fig. 4A). For example, the moisture index is ≈0.6 at 1500 m elevation in the Great Rift Valley, but >1.0 in all sites in western Kenya. Low moisture index in the Great Rift Valley results from low rainfall (typically <900 mm per year). The Lake Victoria basin region is moister than the Great Rift Valley because of higher rainfall (typically >1,300 mm per year). Moisture index is highest in sites of 1,500–1,700 m elevation in western Kenya because the highest rainfall occurs in these areas. Maximum and minimum temperatures are negatively correlated with elevation (Fig. 4B and 4C).

The stepwise multiple regression analysis with *An. gambiae* density as dependent variable identified mean minimum temperatures as the only significant variables (Table 2). *An. arabiensis* density was negatively correlated with moisture index and positively correlated with maximum temperature. *An. funestus* density showed significant correlation with minimum temperature, but not with moisture index (Table 2).

Discussion

This study provided detailed information on the distribution of malaria vectors in western Kenya. In the basin of Lake Victoria, *An. gambiae*, *An. arabiensis*, and *An. funestus* coexist (Mathenge et al. 2001). *An. gambiae* was found in sites <2000 m elevation and *An. arabiensis* in sites of elevation <1,300 m. *An. gambiae* was absent from the Great Rift Valley. *An. funestus* was distributed in the basin of Lake Victoria and the Great Rift Valley, and its abundance is generally lower than that of *An. gambiae* or *An. arabiensis* in most sites.

We further demonstrated that climatic factors strongly affected the distribution and abundance of malaria vectors, particularly moisture index and temperature. Moisture index, calculated as the ratio of

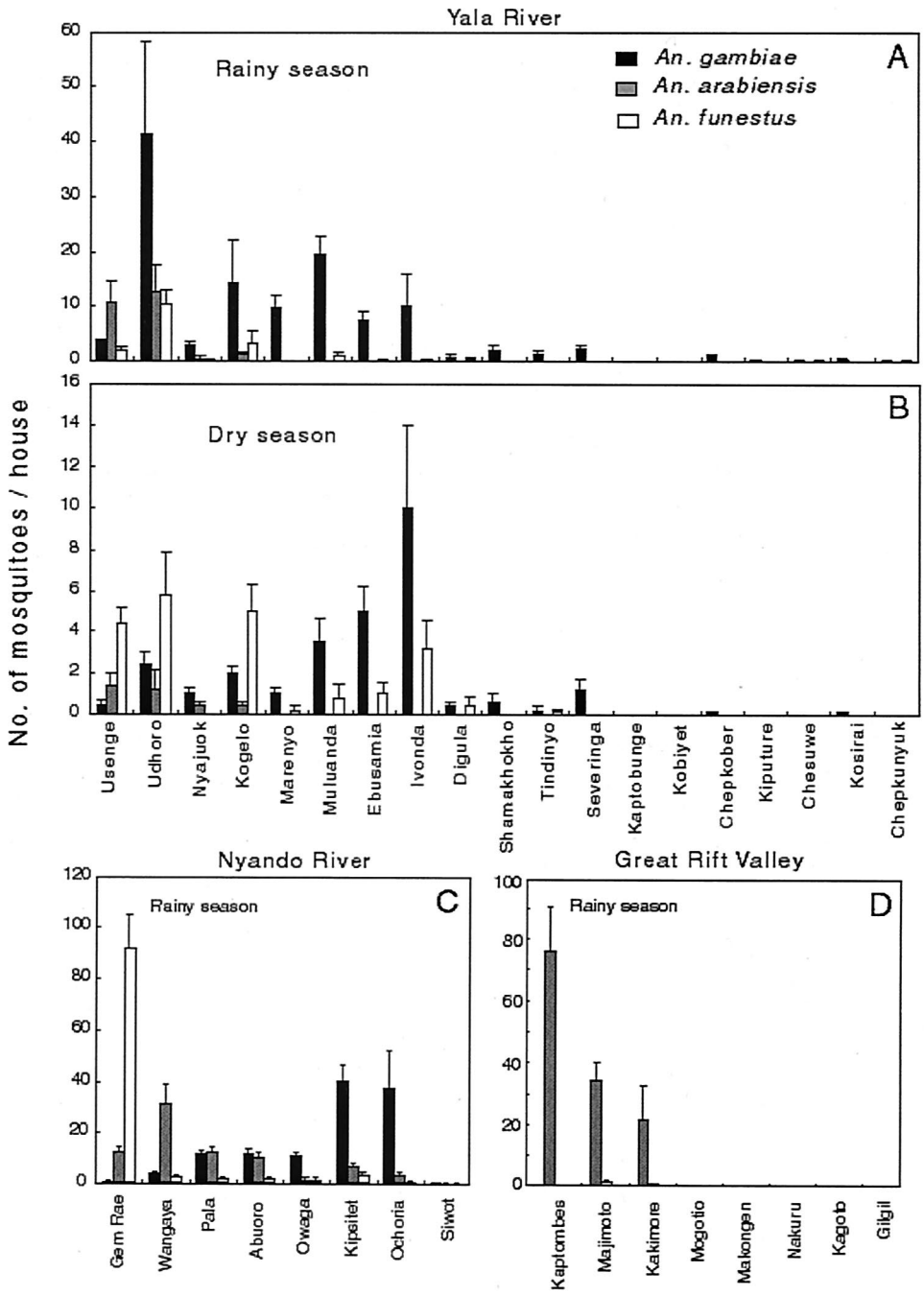

Fig. 2. Densities of *Anopheles gambiae*, *An. arabiensis*, and *An. funestus* in the study sites. (**A**) the Yala River region during the rainy season; (**B**) the Yala River region during the dry season; (**C**) the Nyando River region during the rainy season; and (**D**) the Great Rift Valley during the rainy season.

precipitation to potential evapotranspiration, is higher in western Kenya than in the Great Rift Valley at the same elevation (Fig. 3A). The moisture index of the Great Rift Valley sites investigated in this study is <0.7, suggesting that the valley climate is too dry for *An. gambiae* survival and reproduction. A past study showed that *An. gambiae* dominates over *An. arabiensis* in laboratory colonies kept with high relative hu-

Table 2. Results of stepwise multiple regression analyses for determination of correlation between anopheline mosquito species composition and density and climatic variables

Variable	Percentage of *An. gambiae*		*An. gambiae* density		*An. arabiensis* density		*An. funestus* density	
	b[a]	*P*	b[a]	*P*	b[a]	*P*	b[a]	*P*
Maximum temperature	—	—	—	—	0.660	<0.01	—	—
Minimum temperature	—	—	0.536	<0.01	—	—	0.468	<0.01
Moisture index	0.844	<0.01	—	—	−0.316	<0.01	—	—

The standard partial coefficients and *P*-values are shown only for the variables selected by the stepwise regression analyses.
[a] b is the standard partial regression coefficient.

midity, however, the same study had conflicting results when mixed colonies were exposed to low humidity (Coz 1973). Thus, more detailed studies are needed to clarify the relationships between humidity and ecology of these two species.

Our results are consistent with the findings of Lindsay et al. (1998) that *An. gambiae* is the predominant species in saturated environments while *An. arabiensis* was more tolerant of dry weathers. Using data from West Africa, Lindsay et al. found that the relationship between the relative abundance of *An. gambiae* and moisture index exhibited an "S-shape" curve, and such a general relationship is supported by our data. However, elevation is not a good predictor of *An. gambiae* and *An. arabiensis* distribution because the quantitative relationship between elevation and moisture index varies among geographic regions (Fig. 3A). For example, only *An. gambiae* was found in sites >1,500 m elevation in western Kenya, but *An. gambiae* was absent in sites of same elevation in the Great Rift Valley.

Densities of *An. gambiae* and *An. arabiensis* showed a significant positive correlation with temperature. Anopheline larvae prefer sunlit aquatic habitats, and most *An. gambiae* larval habitats are temporary habitats in western Kenya (Minakawa et al. 1999). Low temperature prolongs larval development and increases mortality rate. Temperature factor contributes to low *An. gambiae* and *An. funestus* densities in high-elevation areas.

We demonstrated that *An. funestus* was more widely distributed than *An. gambiae* and *An. arabiensis.* The abundance of *An. funestus* was much lower than *An. gambiae* or *An. arabiensis* in rainy season in all sites except Awach in the Nyando River region, however its relative abundance was increased dramatically in the dry season and exceeded *An. gambiae* and *An. arabiensis* in some sites (Fig. 2B). This result suggests that *An. funestus* is an important malaria vector that may extend malaria transmission period and bridge malaria transmission between rainy and dry seasons. The fact that *An. funestus* was more abundant than the *An. gambiae* complex in the dry season is probably due to its larval habitat preference. Breeding sites of *An. funestus* are limited to large permanent waters with aquatic vegetation (Ingram and De Meillon 1927,

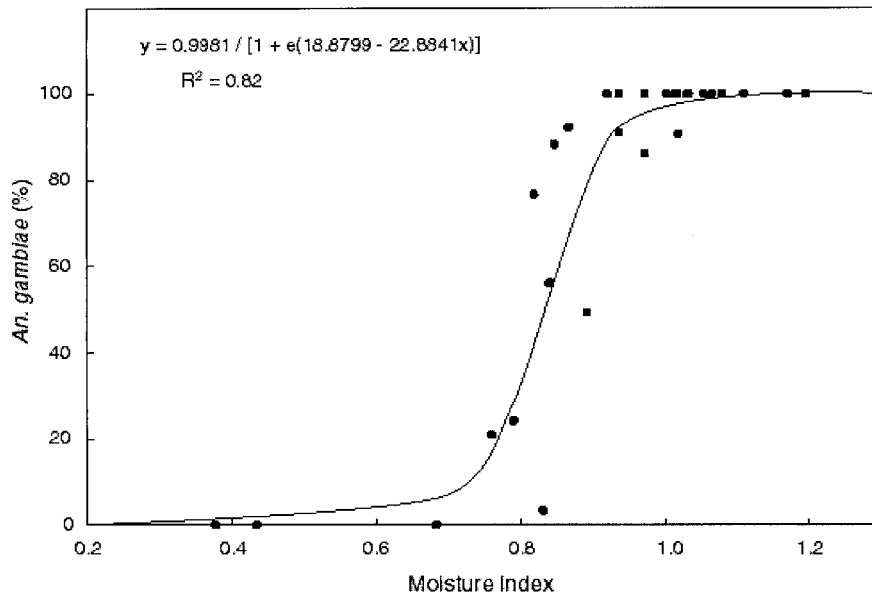

Fig. 3. Relationship between moisture index and relative abundance of *An. gambiae* sensu stricto within *An. gambiae* species complex. The mosquito data were from the rainy season.

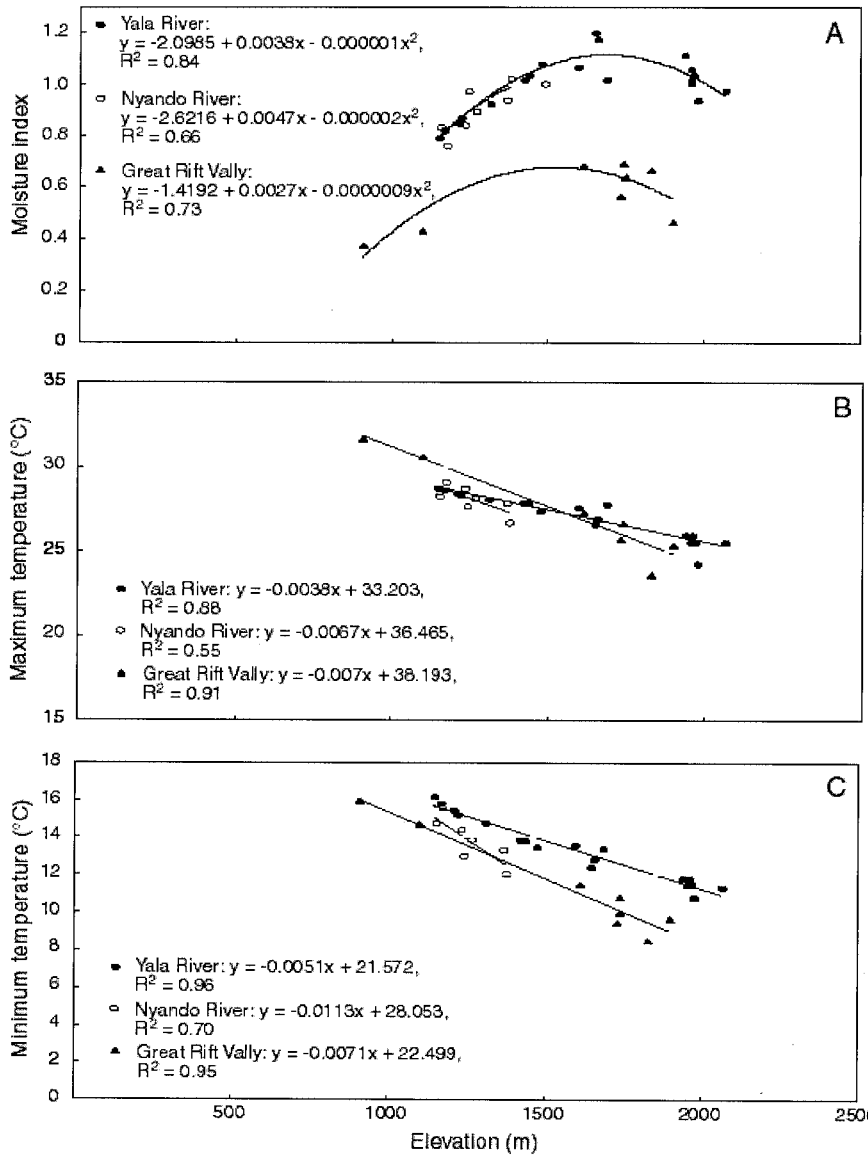

Fig. 4. Relationship between elevation and moisture index (**A**), maximum temperature (**B**), and minimum temperature (**C**) in the Yala River region, the Nyando River region, and the Great Rift Valley.

Evans 1938, Gillies and De Meillon 1968). Such permanent habitats are quite abundant in the basin of Lake Victoria during rainy seasons as well as dry seasons. In dry season, most temporary habitats that *An. gambiae* and *An. arabiensis* use are dried out, and thus the *An. gambiae* complex density is dramatically reduced (Minakawa et al. 2001).

Our results on the distribution of *An. gambiae* and *An. arabiensis* in Kenya have implications on the population genetic structure of anopheline mosquitoes. Lehmann et al. (1999, 2000) demonstrated that *An. gambiae* populations from western Kenya were highly differentiated genetically from Kenyan coastal populations, suggesting that the Great Rift Valley plays an important role in limiting *An. gambiae* gene flow. Our results support the hypothesis that the Great Rift Valley is an important barrier for *An. gambiae* movement between coastal region and western Kenya because it is too dry and not suitable for *An. gambiae.* However, *An. arabiensis* does not inhabit the high-elevation mountains in western Kenya and thus may limit the gene flow of *An. arabiensis.* Our analysis showed that gene flow between the Great Rift Valley and the basin of Lake Victoria was modest for *An. arabiensis* (G. Yan, unpublished data).

The results also have implications on the potential impacts of climate changes on malaria vector distribution and malaria transmission. For example, micro-

climate changes brought about by land use changes may lead to increased *An. gambiae* density in high-elevation areas, and areas previously unsuitable for anopheline mosquitoes may now be inhabited (Lindblade et al. 2000b). Consequently, active malaria transmission may be established in highlands. Indeed, malaria outbreaks have occurred in multiple sites in Kenyan and Ugandan highlands in the past decade (Malakooti et al. 1998; Lindblade et al. 2000a; Githeko and Ndegwa 2001). Because malaria transmission in highlands is unstable, establishing an early warning system of malaria outbreaks in these areas would be particularly useful for malaria prevention and preparation of intervention strategies (Lindblade et al. 2000a; Githeko and Ndegwa 2001; Hay et al. 2001; Thompson and Connor 2001). Equally important, understanding how land use and other climatic factors affect malaria vector distribution and malaria transmission will provide a sound basis for formulating effective environmental management policies for malaria prevention.

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