EFFECTS OF MICROCLIMATIC CHANGES CAUSED BY DEFORESTATION ON THE SURVIVORSHIP AND REPRODUCTIVE FITNESS OF ANOPHELES GAMBIAE IN WESTERN KENYA HIGHLANDS

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Abstract. Land use changes have been suggested as one of the causes of malaria epidemics in the African highlands. This study investigated the effects of deforestation-induced changes in indoor temperature on the survivorship and reproductive fitness of Anopheles gambiae in an epidemic prone area in the western Kenya highlands. We found that the mean indoor temperatures of houses located in the deforested area were 1.2°C higher than in houses located in the forested area during the dry season and 0.7°C higher during the rainy season. The mosquito mortality rate was highly age-dependent regardless of study site or season. Mosquitoes that were placed in houses in the deforested area showed a 64.8–79.5% higher fecundity than those in houses located in the forested area, but the median survival time was reduced by 5–7 days. Female mosquitoes in the deforested area showed a 38.5–40.6% increase in net reproductive rate and an 11.6–42.9% increase in intrinsic growth rate than those in the forested area. Significant increases in net reproductive rate and intrinsic growth rate for mosquitoes in the deforested area suggest that deforestation enhances mosquito reproductive fitness, increasing mosquito population growth potential in the western Kenya highlands. The vectorial capacity of An. gambiae under study was estimated at least 106% and 29% higher in the deforested area than in the forested area in dry and rainy seasons, respectively.

INTRODUCTION

Mosquito survivorship and fecundity are important determinants of population growth dynamics. Survivorship of malaria vectors is also one of the most important factors of vectorial capacity, and thus it has a profound effect on the transmission and epidemiology of vector-borne diseases. For example, an anopheline mosquito needs to survive beyond the extrinsic incubation period of the Plasmodium parasites to be able to transmit malaria; more potential hosts would be bitten if a competent mosquito lives longer. Fecundity, measured by the number of offspring an individual mosquito can produce, is a major fitness trait. Mosquito survivorship and fecundity may be affected by environmental factors such as temperature and humidity. A higher ambient temperature may facilitate blood meal digestion, reduce the length of the gonotrophic cycle, and change the lifetime fecundity of a mosquito. The western Kenya highlands, where ambient temperature is relatively low, have experienced frequent malaria outbreaks in the last two decades, and malaria is a major public health concern especially because malaria parasites are increasingly resistant to anti-malarial drugs. The areas with an altitude greater than 1,500 m above sea level are generally considered as highlands, where climate has marginal conditions for malaria transmission. Several hypotheses, including global warming, climate variability, land use changes, and antimalarial drug resistance, have been proposed as explanations for the emergence of malaria epidemics in East African highlands. Previous studies showed close associations between climate variability and malaria outbreak events, and there were significant spatial variations in the sensitivity of malaria occurrence to climate variability. While climate variability is expected to have a regional effect on malaria transmission, environmental changes such as deforestation and swamp reclamation may affect local microclimatic conditions in a way that favors malaria transmission. For example, Matola et al. suggested that deforestation in the Usambara Mountains of Tanzania could have been responsible for the observed increases in local malaria transmission at high altitude. Lindblad et al. reported that maximum and minimum temperatures were significantly higher in communities bordering cultivated swamps than those near the natural swamps in southwestern Ugandan highlands.

The East African highlands are a fragile ecosystem that is under great pressure from rapidly increasing human populations. The areas have been experiencing dramatic land use changes such as deforestation and swamp cultivation for subsistence agriculture, growing cash crops, and firewood acquisition. For example, Malava forest, a tropical rain forest in Kakamega district, western Kenya, has been shrunk because of deforestation from 150 km² in 1965 to 86 km² in 1997. In the highlands of Eastern Africa, 2.9 million hectares of forest has been cleared between 1981 and 1990, representing an 8% reduction in forest coverage in one decade. Deforestation could modify the microclimate of malaria vectors in the highlands in subtle ways, but such subtle microclimatic changes may have a large effect on mosquito survivorship and fitness. We hypothesize that land use changes, especially deforestation in the western Kenyan highlands, significantly alter the microclimatic conditions of mosquito resting sites that may significantly affect the life history traits of the vectors. The objectives of this study were to quantify the effects of deforestation on the microclimates of residents’ houses where blood-fed anopheline mosquitoes rest and to determine how this may change mosquito survival and reproductive fitness. The experiments were conducted in the Kakamega District, western Kenya. The results of this study are important for assessing the impact of land cover and land use changes on malaria risks in African highlands.

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MATERIALS AND METHODS

Study sites. The study was conducted in Iguhu village (34°45′ E and 0°10′ N; 1,430–1,580 m above sea level), Kakamega district, western Kenya. For comparison, the same experiments were conducted at a lowland site, Kisian village (34°75′ E and 0°10′ S; 1,190 m above sea level), Kisumu district, western Kenya. The average minimum and maximum temperatures during 1970–2000 were 13.8°C and 28.0°C in Kakamega and 15.0°C and 28.4°C in Kisian, respectively. The dry season in both sites is from January to March, and the long rainy season is from June to August. The average annual rainfall was approximately 1,950 mm in Kakamega and 1,400 mm in Kisian. Yala River transects the Kakamega site and most mosquito breeding takes place in cultivated swamps in the valley and at the edges of the streams.16 The study area includes a mosaic of land use types. The hillside is mostly maize plots interspersed with patches of tea plantation, whereas several swamps are located along the Yala River valley. A portion of natural forest is remained in the east side of the study area, constituting about 15% of the total area.21 In this study, we used randomly selected houses in the forested area and deforested area in Iguhu. Forested area is defined as the area with a tree canopy cover more than 60%, whereas a deforested area was a forested area but had been deforested recently and has less than 10% canopy coverage. The lowland site at Kisian is located on the shore of Lake Victoria. The land cover type in Kisian is primarily farmland with little tree canopy coverage, so the entire site was classified as deforested.

Experimental design. Anopheles gambiae larvae were collected from Iguhu and were raised to F2 adults in an insectary in Kisian. One hundred newly emerged F2 females and 100 males were placed in a 30 × 30 × 30-cm metal-framed cages covered with nylon netting. Cages were suspended from the roof, 2 m above the ground, in the bedrooms of the selected houses. All houses had iron-sheet roofs. During the experiment, there were no cooking activities, and no use of mosquito coils, indoor insecticide sprays, or insecticide-treated bed nets was observed in the bedrooms. Grease was smeared on the suspension twine to prevent ants from reaching and feeding on the mosquitoes. Human blood was provided to the mosquitoes for about 15 minutes every other morning. An oviposition substrate consisting of a petri dish lined with a filter paper disk on wet cotton wool was provided in each cage for oviposition. A cotton wool soaked in 10% sucrose solution was supplied to the mosquitoes daily. The number of eggs laid was counted under a dissecting microscope and recorded daily to determine fecundity. Dead male and female mosquitoes were recorded and removed from the cage daily. In the dry season (January–April 2004) in the highland area, the experiments were repeated in three houses in the forested area and three in the deforested area. During the long rainy season (June–August 2004), in both the highland and lowland sites, the experiments were repeated in four houses in each condition (forested highland, deforested highland, and deforested lowland). The experimental houses were randomly selected inside forested area (about 100 m from forest edge) and in the deforested area in Iguhu. The distance between houses in forested and deforested area is about 800 m, and they were at the same elevation. Houses near the campus of Center for Vector Biology and Control Research, Kenya Medical Research Institute in Kisian, western Kenya were randomly selected for lowland site studies.

Climate data collection. HOBO data loggers (Onset Computer Corp., Bourne, MA) were placed inside the experimental houses to record temperature and relative humidity hourly from February 2 to April 29 (dry season) and from June 15 to September 2 (rainy season) of 2004. The data loggers were suspended from the roof, 2 m above the ground. Outdoor temperature was recorded using HOBO data loggers placed in standard meteorological boxes 2 m above the ground for the experiment periods. At the lowland site (Kisian), indoor temperatures were recorded from the three houses from June 30 to September 20, 2004. The data were offloaded using a Hobo Shuttle Data Transporter (Shuttle; Onset Computer Corp.) and downloaded to the computer using BoxCar Pro 4.0 (Onset Computer Corp.).

Data analysis. Daily maximum and minimum temperature and relative humidity were obtained from hourly temperature and humidity data recorded throughout the experimental period. The daily mean temperature and relative humidity are the arithmetic means of the 24 hourly temperature and relative humidity records of a day. Because indoor and outdoor microclimate profiles among the selected houses in each area were similar, in each area and for each season the indoor data were pooled, and the outdoor data were pooled. Analysis of variance (ANOVA) with repeated measure was conducted to determine the effects of land cover and season on outdoor and indoor temperature and relative humidity. Average age-specific survivorship of female mosquitoes was calculated over all houses for each area and each season. Differences in mean survivorship between forested and deforested areas, and between dry and rainy seasons, were tested using the non-parametric Friedman $\chi^2$ test.22 To determine whether mosquito mortality rate is higher in an old-age group than in a young-age group, age-dependent mortality was tested using the Gompertz model, $\mu_x = a e^{bx}$ where $\mu_x$ is mortality rate at age $x$, $a$ is baseline mortality, and $b$ represents the rate of change in mortality with age.22 If $b$ is significantly larger than 0, mosquito mortality rate increases with aging. Parameters $a$ and $b$ were estimated for highland and lowland sites in dry and rainy seasons separately through regression analysis between natural logarithm of $\mu_x$ and age $x$, and the statistical significance of parameter $b$ was determined. The $t$ test was used to determine the statistical difference between the two $b$ values so that to compare whether the rate of change in age-specific mortality varied significantly between forested and deforested areas and between dry and rainy seasons. The analysis was conducted using JMP statistical software.24 Based on daily survivorship and fecundity schedule, we calculated the net reproductive rate, $R_0$, for mosquitoes in different land use types in both dry and rainy seasons. Net reproductive rate is defined as the average number of offspring a female individual in a population will produce in her lifetime and is calculated as $R_0 = \Sigma(l_i m_i)$, where $l_i$ is the age-specific survivorship, and $m_i$ is the age-specific fecundity per mosquito.25,26 We also plotted the daily reproductive rate over the experimental periods. Per-capita intrinsic growth rate, defined as the number of progeny born to each female mosquito per unit of time, was calculated as $r = Ln(R_0)/G$, where $G = \Sigma l_i m_i x / \Sigma l_i m_i x$, and $x$ is mosquito age.25,26 The non-parametric Wilcoxon test was used to compare differ-
ences in fecundity, net reproductive rate, and intrinsic growth rate between forested and deforested areas and between highland and lowland. Only female mosquito life history traits were considered in this analysis even though male mosquitoes were also present in the cages. In the case of multiple comparisons were conducted, the significant level was adjusted using the Bonferroni method.

To evaluate the possible effects of indoor temperature change and changes in adult mosquito survivorship and fecundity because of land use and land cover on vectorial capacity, we used Macdonald's formula: vectorial capacity \(= \frac{ma^p}{1-e^{-\gamma t}}\), where \(m\) is the relative density of vectors in relation to human, \(a\) is the average number of men bitten by one mosquito in 1 day, \(p\) is the proportion of vectors surviving per day, and \(\gamma\) is the duration of sporogony in days. Vectorial capacity is the number of future infections that will arise from one current infective case. Vector abundance was obtained from the population dynamics data from the study area in the period of June 2003 to June 2004. Parameter \(a\) was calculated as 2/first gonotrophic cycle duration that we estimated from the same study sites, assuming double feeding is required for one gonotrophic cycle. \(P\) was estimated from the present adult survivorship data assuming a constant daily survival rate, which is an approximation to observed age-dependent survivorship (see below). The duration of sporogony was calculated as \(T(t - t_{\text{min}})\), where \(T = 111\) degree-days and \(t_{\text{min}} = 16.5^\circ\text{C}\), and \(t\) is mean indoor temperature obtained from this study.

**RESULTS**

**Effects of deforestation on outdoor and indoor temperature and relative humidity.** The average outdoor temperature was 0.4°C higher in the deforested area than in the forested area during both dry and rainy seasons (ANOVA, \(F_{1,38} = 10.05, P = 0.002\) and \(F_{1,74} = 47.82, P < 0.0001\) for dry season and rainy season, respectively). The average outdoor temperatures in the deforested area were 1.2°C higher than in the forested area during the dry season (ANOVA, \(F_{1,66} = 151.04, P < 0.0001\); Table 1) and 0.7°C higher during the rainy season (ANOVA; \(F_{1,66} = 20.26, P < 0.0001\); Table 1). Overall, the outdoor temperature profile in houses located in the forested area was more stable than that in houses in deforested area in both dry and rainy seasons (Figure 1).

The average outdoor temperature in the lowland area was 3.1°C higher than the highland deforested area during the rainy season (ANOVA, \(F_{1,22} = 225.34, P < 0.0001\); Table 1). The average outdoor temperature was 2.8°C higher (ANOVA, \(F_{1,66} = 252.95, P < 0.0001\); Table 1).

Land cover types also affected indoor relative humidity in the highland. For example, the mean indoor relative humidity in the deforested area was about 7% lower than in the forested area during the dry season (68.5% versus 75.6%; ANOVA, \(F_{1,59} = 73.81, P < 0.0001\)) and about 3% lower during the rainy season (69.4% versus 72.2%; \(F_{1,66} = 16.85, P < 0.001\)).

**Figure 1.** Dynamics of daily indoor maximum, minimum, and mean temperature in Kakamega, western Kenya highland. Day 1 in the dry and rainy seasons refers to February 2, 2004 and June 15, 2004, respectively.

**Table 1**

Survivorship and fecundity of *An. gambiae* mosquitoes in different land cover types in western Kenya highland and lowland sites

<table>
<thead>
<tr>
<th>Area</th>
<th>Season</th>
<th>Land cover type</th>
<th>Mean indoor temperature (°C)</th>
<th>Mean outdoor temperature (°C)</th>
<th>Median survival time (days)</th>
<th>Gompertz model parameters*</th>
<th>Fecundity†</th>
<th>Mean net replacement rate (per generation)</th>
<th>Intrinsic per-capita growth rate (per generation)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Highland</td>
<td>Dry</td>
<td>Forested</td>
<td>22.6 ± 0.5</td>
<td>20.7 ± 1.3</td>
<td>44.1 ± 1.3</td>
<td>0.005</td>
<td>0.043</td>
<td>19.3 ± 5.9</td>
<td>527.7 ± 93.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Deforested</td>
<td>23.8 ± 0.7</td>
<td>21.1 ± 1.4</td>
<td>39.0 ± 1.3</td>
<td>0.007</td>
<td>0.042</td>
<td>31.8 ± 2.9</td>
<td>742.0 ± 13.9</td>
</tr>
<tr>
<td></td>
<td>Rainy</td>
<td>Forested</td>
<td>21.5 ± 0.5</td>
<td>18.8 ± 1.1</td>
<td>30.6 ± 0.8</td>
<td>0.007</td>
<td>0.056</td>
<td>15.1 ± 2.2</td>
<td>314.0 ± 28.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Deforested</td>
<td>22.2 ± 0.8</td>
<td>19.2 ± 1.1</td>
<td>23.9 ± 0.6</td>
<td>0.010</td>
<td>0.075</td>
<td>27.1 ± 3.0</td>
<td>434.8 ± 43.8</td>
</tr>
<tr>
<td>Lowland</td>
<td>Rainy</td>
<td>Forested</td>
<td>25.0 ± 0.4</td>
<td>22.3 ± 0.4</td>
<td>21.8 ± 1.1</td>
<td>0.017</td>
<td>0.031</td>
<td>20.1 ± 3.8</td>
<td>346.0 ± 4.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Deforested</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.237 ± 0.02</td>
</tr>
</tbody>
</table>

*SD for mean indoor and mean outdoor temperatures, age-dependent mortality, median survival time, fecundity, mean net replacement rate, and mean intrinsic rate of growth is shown.

† Fecundity is measured in number of female progeny per female per day.

‡ \(R_n\) is the mean net replacement rate (number of offspring per female per generation).

§ \(r\) is intrinsic per-capita growth rate (number of offspring per female per day).
Effects of deforestation on mosquito survivorship. Mosquitoes in the forested area lived longer than those in the deforested area in both dry and rainy seasons in the highland (Figure 2). Specifically, the median survival length was 44.1 days in the forested area and 39.0 days in the deforested area during the dry season ($\chi^2 = 13.11$, df = 1, $P < 0.0001$; Table 1). During the rainy season, the median survival length was 30.6 days in the forested area and 23.9 days in the deforested area ($\chi^2 = 73.54$, df = 1, $P < 0.0001$). In the lowland deforested area, the median survival length was 21.8 days in the rainy season, which was significantly shorter than that in the deforested area in the highland (23.9 days; $\chi^2 = 27.16$, df = 1, $P < 0.0001$).

We found that adult mosquito mortality is age-dependent in both dry and rainy seasons in the highland (Figure 3). Significant positive values of $b$ (the rate of change in mortality with age) in the Gompertz model suggest that older mosquitoes had a higher mortality rate than younger mosquitoes (Table 1). During the dry season, the rates of change in mortality with age were similar between the deforested and forested areas ($t = 0.21$, df = 140, $P = 0.831$; Figure 3). However, during the rainy season, the rate of change in mortality in the deforested area was significantly higher than that in the forested area ($t = 2.46$, df = 102, $P = 0.015$; Figure 3). Also, the rates of change in mortality with age were significantly higher in the rainy season than in the dry season in both the deforested area ($t = 4.31$, df = 110, $P < 0.001$) and the forested area ($t = 2.67$, df = 132, $P = 0.008$).

Effects of deforestation on mosquito fecundity. In the highland area during the dry season, female mosquitoes placed in the deforested area increased average daily fecundity by 64.8% over mosquitoes in the forested area ($t = 3.86$, df = 1, $P < 0.05$; Table 1). During the rainy season, mosquito fecundity was 79.5% higher in the deforested area than in the forested area ($t = 5.32$, df = 1, $P < 0.05$; Table 1). Mosquito fecundity in the deforested lowland site was similar to that in

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**Figure 2.** Survivorship dynamics of *An. gambiae* in the rainy season (A) and the dry season (B) in western Kenya.

**Figure 3.** Age-specific *An. gambiae* mortality in natural logarithm scale in western Kenya highland deforested area during the dry season (A); forested area during dry season (B); deforested area during rainy season (C); and forested area during rainy season (D). The value of $R^2$ in each graph represents the proportion of variance in age-specific mortality explained by age. $P$ is the significance level of Gompertz model fitting.
the deforested highland site during the rainy season ($\chi^2 = 3.12, df = 1, P = 0.08$; Table 1).

**Effects of deforestation on mosquito net reproductive rate and intrinsic growth rate.** Despite the shorter life span of female mosquitoes in the deforested highland area, the mean net reproductive rate, $R_0$, was 40.6% higher in the deforested area than in the forested area during the dry season ($\chi^2 = 3.97, df = 1, P < 0.05$; Table 1). During the rainy season, $R_0$ was 38.5% higher in the deforested area than in the forested area in highland ($\chi^2 = 5.32, df = 1, P < 0.05$, Table 1). $R_0$ in the deforested lowland was 25.7% higher than in the deforested highland ($\chi^2 = 4.50, df = 1, P < 0.05$). The temporal dynamics of $R_0$ showed that *An. gambiae* females in the forested area had a lower daily net reproductive rate than those in the deforested area, but they exhibited a longer egg laying period (Figure 4). During the dry season, per capita intrinsic growth rate, $r$, was 11.6% higher in the deforested areas than in the forested areas (Table 1), but the difference was not significant ($\chi^2 = 0.05, df = 1, P > 0.05$). However, during the rainy season, $r$ was 42.9% higher in the deforested area than the forested area ($\chi^2 = 5.39, df = 1, P < 0.05$; Table 1). Mosquitoes in the open lowland area showed a significantly higher intrinsic growth rate than in the deforested highland ($\chi^2 = 4.58, df = 1, P < 0.05$).

**Effect of deforestation on vectorial capacity.** In the dry season, female *A. gambiae* density was estimated about 0.5 mosquitoes per person per day in the highland area, and it increased to about 10 in the rainy season. In the lowland area, vector density was estimated about 20 in the rainy season. Assuming that vector density in forested and deforested areas in the highland was same, using the parameters specific in Table 2, vectorial capacity was estimated to be twice higher in the deforested area than in the forested area in the dry season and 29% higher in the rainy season in the highland (Table 2). In the lowland, vectorial capacity was estimated at 18.836 in the rainy season, about 15-fold higher than the highland deforested area (Table 2). Therefore, deforestation increases vector capacity in the highland, and vectorial capacity in the lowland is substantially higher than in the highland.

**DISCUSSION**

In this study, we showed that deforestation in western Kenya led to an increase in indoor temperature, and consequently, enhanced the net reproductive rates of *An. gambiae* mosquitoes. This phenomenon was consistent over both dry and rainy seasons. Deforestation enhanced vectorial capacity by 106% and 29% in the dry and rainy seasons in the highland, respectively, under the conservative assumption that the vector abundance in the forested and deforested areas are the same. We also found that the survivorship and fecundity of female adult mosquitoes in the dry season were better than in the rainy season, at least under the experimental conditions that we used. Consequently, the net reproductive rate in the dry season was higher than in the rainy season. The seasonal difference in survivorship and fecundity is likely caused by higher ambient temperature in the dry season than in the rainy season.

Land cover changes may affect radiation budget and energy balance of land surface. Morphologic changes in vegetation can change albedo, and physiologic changes in vegetation can alter latent heat flux. Skinner and Majorowicz found that the areas in northwestern Canada to southcentral United States exhibiting the highest ground surface temperature increases are the areas where extensive land cover changes have occurred, such as the clearing of forests, increased forest fire activity, and conversion of prairie grassland to agricultural land. Bounoua et al. found that large-scale conversion of forest and grassland to cropland warms surface temperature by 0.8°C year around in the tropics and subtropics. Lindblade et al. also found that changes in the land cover in areas surrounding cultivated swamps led to an increase in minimum and maximum temperature by 0.8-0.9°C in southwestern Uganda. Our finding that the average indoor temperature in houses in a deforested area was 0.7-1.2°C higher than that in houses in a forested area is consistent with these studies.

Higher temperature causes faster blood meal digestion, thereby shortening the length of the gonotrophic cycle of mosquitoes. For example, compared with *An. gambiae* mosquitoes placed in a forested area, the duration of *An. gambiae* first and second gonotrophic cycles was shortened by 1.7 and 0.9 days during the dry season and by 1.5 and 1.4 days during the rainy season, respectively, when they were placed in de-
Table 2
Estimated vectorial capacity of An. gambiae in forested and deforested areas in western Kenya highland and lowland

<table>
<thead>
<tr>
<th>Area</th>
<th>Season</th>
<th>Land use type</th>
<th>m</th>
<th>P</th>
<th>N</th>
<th>First gonotrophic cycle duration</th>
<th>a</th>
<th>Vectorial capacity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Highland</td>
<td>Dry</td>
<td>Forested</td>
<td>0.5</td>
<td>0.940</td>
<td>19.20</td>
<td>4.6</td>
<td>0.435</td>
<td>0.991</td>
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<td>0.928</td>
<td>15.21</td>
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<td>0.690</td>
<td>2.043</td>
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<tr>
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<td>Forested</td>
<td>10</td>
<td>0.927</td>
<td>22.20</td>
<td>10.1</td>
<td>0.198</td>
<td>0.961</td>
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<tr>
<td></td>
<td></td>
<td>Deforested</td>
<td>10</td>
<td>0.919</td>
<td>19.47</td>
<td>8.6</td>
<td>0.233</td>
<td>1.236</td>
</tr>
<tr>
<td>Lowland</td>
<td>Rainy</td>
<td>Deforested</td>
<td>20</td>
<td>0.923</td>
<td>13.06</td>
<td>4.3</td>
<td>0.465</td>
<td>18.863</td>
</tr>
</tbody>
</table>

m is the relative density of vectors in relation to human, P is the proportion of vectors surviving per day, a is the average number of men bitten by one mosquito in one day, and N is the duration of sporogony in days. See text for details on data source and the assumptions made for calculating each variable.

We found that deforestation caused mosquitoes to feed more often and lay eggs more frequently in a deforested area. This may explain why mosquitoes placed in deforested areas had a higher average daily fecundity. The higher mortality of mosquitoes in the deforested areas may be caused by higher metabolism and higher reproductive output. In Drosophila, a higher reproductive output is negatively correlated with longevity. In addition, lower humidity in houses located in the deforested area may have negatively affected mosquito survival because An. gambiae mosquitoes are adapted to humid environments. Although mosquitoes in the highland deforested area exhibited a reduced survivorship, they showed a significantly higher net reproductive rate and per-capita intrinsic growth rate than those in the forested area. This is primarily caused by the higher fecundity and shorter generation time exhibited by mosquitoes in the deforested area. Life table studies by Morgan et al. in the pea aphid, Acylithosiphon pisum, showed that the intrinsic rate of growth increased with temperature. Bayhan et al. found that Aphis punicae also showed an increased reproductive rate with an increase in temperature.

Okech et al. in their study with An. gambiae in the lowland of western Kenya, also reported that mean mosquito survival was 33 days for mosquitoes fed on sugar and blood. Takken et al. used the marker-release-recapture method and estimated that daily survival rates of An. gambiae s.l. were 0.78 in a rural area near Ifakara, Tanzania. Our estimates of mosquito longevity were longer than those published studies, partly because mosquitoes in our study were provided blood feeding opportunities and sugar every 2 days, and humidity at our highland study site was higher. For example, median survival time of mosquitoes placed in the lowland area was 2 days shorter than that in the highland. Gary and Forster found that An. gambiae mosquitoes fed on blood and sugar had a median survival time of 29 days under insectary conditions, significantly longer than those fed on either sugar or blood alone. Our estimate of mosquito longevity could be higher than longevity found under natural conditions because access to a human host and to additional food (sugar) could be limited in nature. We found that An. gambiae mosquitoes exhibited age-dependent mortality. That is, older mosquitoes showed a higher daily mortality rate than younger mosquitoes. Whether age-dependent mortality occurs in An. gambiae under natural conditions needs to be determined.

Our results have implications for understanding the effect of land cover changes on malaria transmission in the African highlands. Earlier studies found that deforestation can increase larval productivity, accelerate larval development time, and increase larval pupation rate. Thus, adult mosquito density is expected to be higher in the deforested area and in the forested area. More importantly, increased indoor temperature caused by deforestation shortens mosquito gonotrophic cycle length and thus increases biting frequency, and shortens the sporogonic development of Plasmodium parasite in mosquitoes (Y. Afrane, unpublished data). Because vectorial capacity is particularly sensitive to mosquito biting frequency and parasite sporogonic development duration, vectorial capacity in the deforested area is substantially increased over the forested area. Therefore, this study adds to the evidence that deforestation in East African highland enhances malaria transmission.

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