

Effects of Microclimatic Changes Caused by Land Use and Land Cover on Duration of Gonotrophic Cycles of *Anopheles gambiae* (Diptera: Culicidae) in Western Kenya Highlands

Author(s): Yaw A. Afrane, Bernard W. Lawson, Andrew K. Githeko, and Guiyun Yan

Source: Journal of Medical Entomology, 42(6):974-980.

Published By: Entomological Society of America

DOI: [http://dx.doi.org/10.1603/0022-2585\(2005\)042\[0974:EOMCCB\]2.0.CO;2](http://dx.doi.org/10.1603/0022-2585(2005)042[0974:EOMCCB]2.0.CO;2)

URL: [http://www.bioone.org/doi/](http://www.bioone.org/doi/full/10.1603/0022-2585%282005%29042%5B0974%3AEOMCCB%5D2.0.CO%3B2)

[full/10.1603/0022-2585%282005%29042%5B0974%3AEOMCCB%5D2.0.CO%3B2](http://www.bioone.org/doi/full/10.1603/0022-2585%282005%29042%5B0974%3AEOMCCB%5D2.0.CO%3B2)

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Effects of Microclimatic Changes Caused by Land Use and Land Cover on Duration of Gonotrophic Cycles of *Anopheles gambiae* (Diptera: Culicidae) in Western Kenya Highlands

YAW A. AFRANE,^{1, 2} BERNARD W. LAWSON,² ANDREW K. GITHEKO,¹ AND GUIYUN YAN³

J. Med. Entomol. 42(6): 974–980 (2005)

ABSTRACT Studies were carried out at a malaria epidemic-prone highland site in western Kenya to determine the effects of deforestation-caused microclimate change on the duration of the gonotrophic cycle of the malaria vector *Anopheles gambiae* Giles. Gonotrophic cycle duration was measured using field-collected F₁ *A. gambiae* females. Average ambient temperature in the deforested area of Kakamega (elevation 1,430–1,580 m above sea level), western Kenya, was 0.5°C higher than that of the forested area over a 10-mo period. During the dry season, deforested areas showed an increased mean indoor temperature of 1.8°C, and a shortened duration of the mosquitoes' first and second gonotrophic cycles, by 1.7 d (59%) and 0.9 d (43%). During the rainy season, the average indoor temperature of houses located in the deforested area was 1.2°C higher than in houses in the forested area. The duration of the first and second gonotrophic cycles was shortened by 1.5 d (17%) and 1.4 d (27%), respectively, in the deforested highland site. A shorter mosquito gonotrophic cycle implies increased daily biting frequency and thus increased vectorial capacity. Together with evidence that deforestation reduced *A. gambiae* larva-to-adult developmental time and increased larval and adult survivorship, this study suggests that deforestation can further enhance malaria transmission potential in the highlands through increased indoor temperature and shortened gonotrophic cycle durations of *A. gambiae* mosquitoes.

KEY WORDS deforestation, malaria, microclimate, gonotrophic cycle

Plasmodium falciparum transmitted by *Anopheles gambiae* Giles and *Anopheles funestus* Giles has caused frequent malaria outbreaks in the western Kenya highlands in the past two decades (Some 1994, Githeko and Ndegwa 2001, Hay et al. 2002). The epidemics generally occur in areas with an altitude >1,500 m above sea level where ambient temperature is low (Githeko and Ndegwa 2001). Recent malaria epidemics in the highlands are of particular concern and a major public health problem. This is because, during these epidemics, a large number of residents became ill during a short time, and the number of malaria outpatients and inpatients far exceeded the capacity of local clinics or hospitals. Antimalarial drug resistance and delayed or inadequate drug treatment caused a large number of malaria patients to die (Shanks et al. 2000, Omar et al. 2001). Although climate variability was found to be associated with the occurrence of epidemic events (Bouma 2003, Zhou et al. 2004), environmental changes, such as deforestation and swamp cultivation,

also were implicated as potential contributing factors (Walsh et al. 1993, Manga et al. 1995, Lindsay and Martens 1998, Lindblade et al. 2000, Minakawa et al. 2005).

Land use and land cover changes modify the microclimatic conditions of malaria vectors in the highlands. These changes may enhance malaria transmission potential. Matola et al. (1987) suggested that deforestation in the Usambara Mountains of Tanzania might be associated with increases in local malaria transmission. In the southwestern highlands of Uganda, maximum and minimum temperatures were significantly higher in communities bordering cultivated swamps than in those near natural swamps (Lindblade et al. 2000). Deforestation and swamp cultivation have been occurring rapidly in western Kenya highlands. For example, Malava forest, a tropical rain forest in Kakamega district, has shrunk from 150 km² in 1965 to 86 km² in 1997 (Round-Turner 1994, Brooks et al. 1999). This resulted from increased human demand for forest products and increased agricultural cultivation. In the East African highlands, 2.9 million ha of forest was cleared between 1981 and 1990, representing an 8% reduction in forest cover in one decade (FAO 1993).

Small changes in the temperature of malaria vector resting habitats in the relatively cold highlands may

¹ Climate and Human Health Research Unit, Centre for Vector Biology and Control Research, Kenya Medical Research Institute, Kenya.

² Department of Biological Sciences, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana.

³ Department of Biological Sciences, State University of New York at Buffalo, Buffalo, NY 14260.

have significant impacts on the kinetics of mosquito blood digestion. Subsequently, effects may be seen on population reproduction rates through changes in the duration of the gonotrophic cycle (the period between blood feeding and ovipositing). Hematophagous mosquitoes require bloodmeals for egg development, and the rate of bloodmeal digestion is temperature dependent. That is, higher ambient temperatures would lead to faster bloodmeal digestion and thus shorter gonotrophic cycle duration and higher biting frequency by the mosquitoes. The rates of feeding on humans by malaria vectors are an important determinant of vectorial capacity (Service et al. 1986). Moreover, temperature increases because of land cover and land use changes may accelerate the sporogonic development rate of *Plasmodium* parasites and consequently enhance the vectorial capacity of malaria vectors. The objective of the current study is to quantify the effects of deforestation on the microclimate (temperature and relative humidity) of adult *A. gambiae* mosquito resting sites (indoor and outdoor) and the subsequent effects on the duration of the gonotrophic cycles. The experiments were conducted in the Kakamega District of western Kenya where frequent malaria outbreaks were reported (Githeko and Ndegwa 2001). This information is important for assessing the impact of land cover and land use changes on malaria risks in African highlands.

Materials and Methods

Study Sites. The study was performed at a highland site in a 4 by 4-km² area in Iguhu village (34° 45' E and 0° 10' N; 1,430–1,580 m above sea level), Kakamega District, and at a lowland site, Kisian village (34° 75' and E 0° 10' S; 1,190 m above sea level), Kisumu District, western Kenya. The average minimum and maximum temperature during 1970–2000 was 15.0 and 28.4°C in Kisian and 13.8 and 28.0°C in Kakamega, with the hottest season in January–February and the coolest season in July–August. The average annual rainfall was ≈1,400 mm in Kisian and 1,950 mm in Kakamega. The Yala River transects the Kakamega site and most mosquito breeding takes place in cultivated swamps in the valley and also at the edges of the several streams (Minakawa et al. 2005). The study area includes a mosaic of land use types. The hillside is mostly maize plots dotted by patches of tea plantation, whereas several swamps are located along the Yala River valley. A natural forest is located in the east side of the 4 by 4-km² study area, constituting ≈15% of the total area. Three houses in the forested area and three in the deforested area in Iguhu and Kisian were randomly chosen for the following experiments. The tree canopy cover in the forested area was >80 and <10% in the deforested area.

Experimental Design. Mosquitoes used in the experiments described below were from *A. gambiae* F₁ individuals from Iguhu, western Kenya. Two hundred 4-d-old virgin female *A. gambiae* mosquitoes were placed into a 30 by 30 by 30-cm³ cage and bloodfed from a volunteer for 30 min. Those that did not feed

were aspirated out of the cage. An equal number of virgin *A. gambiae* male mosquitoes were introduced into the cages to allow females to mate for 24 h. Cages were suspended from the roof at a distance of 2 m above the ground in resident's bedrooms. All houses had iron sheets as roofing materials, and cooking activities and the use of mosquito coil or spray did not occur in the bedrooms during the experimental period. To prevent ants from reaching and feeding on the mosquitoes, grease was applied to the suspension twines. After 24 h, each of the 100 female blood-fed mosquitoes was transferred into an individual oviposition cup. The oviposition cups, 10 cm in width and 12 cm in height, each contained a piece of filter paper on a wet cotton wool pad as a substrate for oviposition, and the cups were placed on a table inside the resident's bedroom in each of the three houses. Grease barriers were placed on the table legs to prevent ants from entering the oviposition cups. The number of eggs laid per female mosquito during the first gonotrophic cycle was counted under a dissection microscope and recorded. Mosquitoes that laid eggs were given a second bloodmeal to determine the duration of the second gonotrophic cycle. The eggs laid in the second gonotrophic cycle were not counted. The experiments were conducted in Iguhu during the dry season between February and March 2004 and repeated during the rainy season between June and July 2004. Three houses in the forested area and three in the deforested area were used in Iguhu. Thus, in total 300 blood-fed female mosquitoes in each area and season were used.

In the lowland site (Kisian), we followed the same procedure as outlined above in three houses in the rainy season between June and July 2004. The land cover and land use type in Kisian was primarily farmland with little tree canopy coverage, so the entire site was classified as deforested.

Climate Data Collection. At the highland site, HOBO data loggers (Onset Computer Corporation, Bourne, MA) were placed inside each house in Iguhu where the gonotrophic cycle length was measured, to record temperature and relative humidity hourly in the forested and deforested areas from 2 February to 15 March (dry season), and from 15 June to 31 August (rainy season) 2004. The data loggers were suspended from the roof, 2 m above the ground. Outdoor temperature was recorded by placing three HOBO data loggers in standard meteorological boxes, 2 m above the ground for the period from 8 January to 18 October 2004. At the lowland site (Kisian), indoor and outdoor temperatures were recorded from 30 June to 31 August (rainy season) by using the same procedures as described above. These data were offloaded from the data loggers using a Hobo Shuttle Data Transporter (Shuttle, Onset Computer Corporation) and then downloaded to the computer using BoxCar Pro 4.0 (Onset Computer Corporation).

Data Analysis. Monthly average minimum or maximum temperatures were calculated from the daily record of minimum or maximum temperature. The daily mean temperature is the arithmetic mean of the

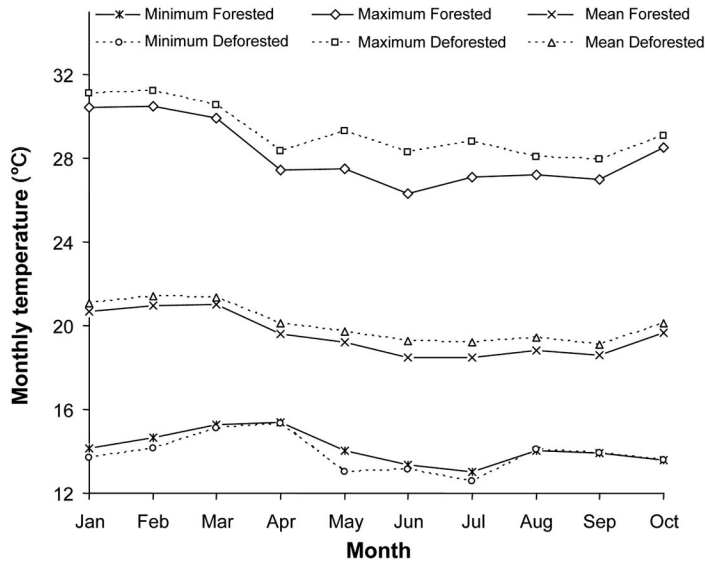


Fig. 1. Monthly mean, maximum, and minimum outdoor temperatures in the forested and deforested area at Iguhu, western Kenya, from January to October 2004.

24 hourly temperature records of a day, and mean monthly temperature is the average of daily mean temperatures. Because temperature and humidity profiles among the three houses within a treatment (forested versus deforested area; indoor versus outdoor) were similar, temperature and relative humidity data were pooled for the three data loggers within a treatment. Paired *t*-tests were conducted to determine the effects of land cover (forested versus deforested) on outdoor and indoor temperature and relative humidity. Mean gonotrophic cycle duration is defined as the average number of days that female mosquitoes took to lay eggs after taking a bloodmeal. We compared the number of eggs laid in each type of land cover and the proportion of mosquitoes that laid eggs, using the χ^2 test. Nonparametric Kruskal-Wallis rank sum tests were used to determine the effects of land cover (forested versus deforested) on the mean duration of the gonotrophic cycle of *A. gambiae*. The *t*-tests were conducted to evaluate the effect of land cover types on fecundity for each season. Fecundity data were square-root transformed. All analyses were conducted using the JMP statistical software (SAS Institute 1994).

Results

Effects of Deforestation on Outdoor Temperature.

Average monthly maximum outdoor temperatures and mean monthly outdoor temperature were significantly higher in the deforested area than in the forested area of the highland site during the study period, January to October 2004 (Fig. 1). In particular, the average monthly temperature during this period in the deforested area was 0.52°C higher than that in the forested area ($t = 10.83$, $df = 9$, $P < 0.001$), and the average monthly maximum temperature was 1.1°C

higher ($t = 6.37$, $df = 9$, $P < 0.001$). However, the average minimum temperature in the deforested area was 0.28°C lower than that in the forested area ($t = 2.77$, $df = 9$, $P = 0.01$; Fig. 1). Therefore, forest canopy coverage plays a buffering role in ambient temperature regulation at the highland site.

Effects of Deforestation on Indoor Microclimate.

Fig. 2 shows the 24-h indoor temperature and relative humidity profile at the highland and lowland sites. The 24-h cycle profile was calculated as the average of the hourly readings of temperature and relative humidity over the dry season or rainy season. During the dry season (February–March), the average indoor temperatures in the deforested area at the highland site were 1.8°C higher than in the forested area ($t = 3.07$, $df = 23$, $P < 0.01$; Table 1). Between 1200 and 1400 hours, indoor temperatures in the deforested area were 7.1–7.6°C higher than in the forested area (Fig. 2A). Similarly, during the rainy season (June–August), mean indoor temperatures in the deforested area at the highland site were 1.2°C higher than that in the forested area ($t = 3.81$, $df = 23$, $P < 0.001$; Table 1), with the maximum temperature difference of 4.5–5.1°C occurring between 1200 and 1400 hours (Fig. 2B). Compared with the lowland site, the mean indoor temperature in the deforested area of the highland site was consistently lower by 1.5–3.0°C, with an average of 2.7°C ($t = 34.78$, $df = 23$, $P < 0.001$; Fig. 2B).

Mean indoor relative humidity in the highland deforested area (64.8%) during the dry season was not significantly different from that in the forested area (64.9%) ($t = 0.03$, $df = 23$, $P > 0.05$). The relative humidity in the highland deforested area fluctuated substantially, and the lowest relative humidity was observed between 1200 and 1400 hours when indoor temperature was also higher (Fig. 2C). In contrast, relative humidity in the forested area during the dry

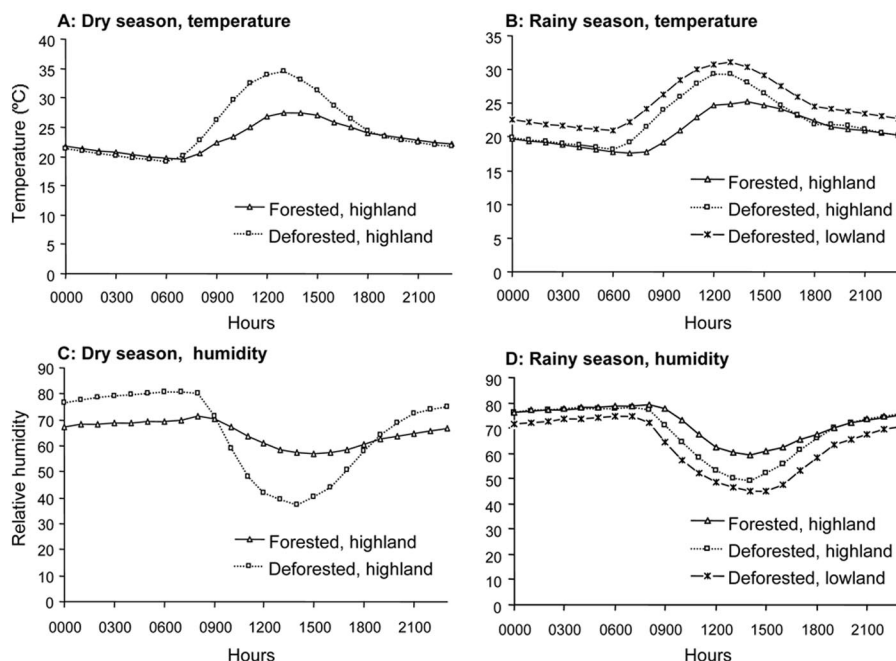


Fig. 2. Mean indoor temperature and relative humidity 24-h daily cycle in houses located in the forested and deforested area in Iguhu, western Kenya. (A) Average hourly temperature during dry season (2 February–15 March 2004). (B) Average hourly temperature during rainy season (15 June–31 August 2004). (C) Average hourly relative humidity during dry season. (D) Average hourly relative humidity during rainy season.

season was more stable. During the rainy season, indoor relative humidity in the forested area during 0800–1700 hours was higher than in the highland deforested area, and the average humidity in the forested area was significantly higher ($t = 4.17$, $df = 23$, $P < 0.001$; Fig. 2D). Compared with the lowland site, the relative humidity in the highland deforested area was consistently higher by $\approx 5.5\%$ ($t = 16.82$, $df = 23$, $P < 0.001$; Fig. 2D) during the rainy season.

Effects of Deforestation on Gonotrophic Cycle Duration. During the dry season, significantly fewer mosquitoes (42.7%) in the highland forested area laid eggs than those in the deforested area (53.7%) ($\chi^2 = 7.27$, $df = 1$, $P < 0.01$; Table 1). The average duration of the first gonotrophic cycle in the forested area was 4.6 d after blood feeding, 1.7 d (59%) longer than those

in the deforested area (2.9 d) ($z = 7.72$, $P < 0.001$; Table 1). The average duration of the second gonotrophic cycle in the forested area was 3.0 d after second bloodmeal, 0.9 d (43%) longer than those in the deforested area (2.1 d) ($z = 3.62$, $P < 0.001$; Table 1).

During the rainy season, there was no significant difference in the proportion of blood-fed mosquitoes that laid eggs during the first gonotrophic cycle between those placed in the highland forested and deforested areas (54.3 versus 60.0%; $\chi^2 = 1.97$, $df = 1$, $P > 0.05$; Table 1). However, the average duration of the first gonotrophic cycle for the mosquitoes in the forested environment was 1.5 d (17%) longer than those in the deforested environment (10.1 versus 8.6 d after blood feeding; $z = 2.19$, $P < 0.05$; Table 1). Similarly, the average length of the second gonotrophic cycle for

Table 1. Duration of the first and second gonotrophic cycles of *A. gambiae* mosquitoes in different land cover types in western Kenya highland and lowland sites

Area	Season	Land cover type	Mean indoor temp (°C)	Mean outdoor temp (°C)	First gonotrophic cycle			Second gonotrophic cycle	
					Proportion of mosquitoes that laid eggs (%)	Mean duration (d)	Mean fecundity	Proportion of mosquitoes laid eggs (%)	Mean duration (d)
Highland	Dry	Forested	23.0 \pm 0.6	20.8 \pm 1.3	42.7	4.6 \pm 2.7	43.4 \pm 19.3	7.3	3.0 \pm 1.1
		Deforested	24.8 \pm 0.8	21.6 \pm 1.4	53.7	2.9 \pm 1.7	62.1 \pm 32.0	7.7	2.1 \pm 0.3
	Rainy	Forested	21.0 \pm 0.9	18.7 \pm 1.1	54.3	10.1 \pm 5.8	85.4 \pm 44.9	22.7	6.6 \pm 2.4
		Deforested	22.2 \pm 0.8	19.2 \pm 0.8	60.0	8.6 \pm 4.9	74.2 \pm 38.5	23.7	5.2 \pm 2.6
Lowland	Rainy	Deforested	24.9 \pm 0.4	22.2 \pm 0.9	67.3	4.3 \pm 2.1	73.7 \pm 34.2	30.4	3.8 \pm 1.7

Field collected F₁ female mosquitoes that had blood fed and mated were used. Standard deviation for mean indoor and mean outdoor temperatures, gonotrophic cycle duration, and fecundity is shown.

the mosquitoes in the forested area was 1.4 d (27%) longer than those in the deforested area (6.6 versus 5.2 d after second bloodmeal; $z = 3.44$, $P < 0.001$; Table 1).

In comparison, the average length of the first gonotrophic cycle was 4.3 d (100%) longer in the highland deforested environment than in the lowland deforested environment ($z = 9.67$, $P < 0.0001$). Similarly, the average length of the second gonotrophic cycle was 1.4 d (37%) longer in the highland site (5.2 versus 3.8 d after second bloodmeal; $z = 3.24$, $P < 0.01$).

To examine whether temperature was a major determinant of gonotrophic cycle length in *A. gambiae*, we conducted linear regression analyses between average indoor temperature and the lengths of the first and second gonotrophic cycles by using the data collected from the highland and lowland sites and from the dry and rainy seasons. We found a highly significant association between the indoor temperature and the lengths of the first gonotrophic cycle ($r^2 = 0.86$, $b = -1.69$, $df = 4$, $P < 0.001$) and of the second gonotrophic cycle ($r^2 = 0.70$, $b = -0.89$, $df = 4$, $P < 0.001$).

Effects of Deforestation on Fecundity. During the first gonotrophic cycle in the dry season, mosquitoes placed in houses located in the forested area exhibited significantly lower fecundity than those in the deforested area (43.4 versus 62.1 eggs; $t = 3.59$, $df = 1$, $P < 0.001$). However, no significant difference in fecundity was observed in the rainy season ($t = 1.55$, $df = 1$, $P > 0.05$). Similarly, mosquitoes produced similar number of eggs when they were placed in the deforested environment in either the highland or lowland sites.

Discussion

In this study, we demonstrated that the average ambient temperature in a deforested area in the western Kenya highlands was $\approx 0.5^\circ\text{C}$ higher than that of a forested area over a 10-mo period. The average indoor temperature of houses located in the deforested area was 1.8 and 1.2°C higher than of those inside the forested area during the dry and rainy seasons, respectively. The relative humidity in the deforested area fluctuated substantially, whereas the humidity in the forested area was more stable. As a consequence of indoor temperature increase, the average duration of the first gonotrophic cycle of *A. gambiae* mosquitoes in the deforested area was shortened by 1.7 and 1.5 d and by 0.9 and 1.4 d for the second gonotrophic cycle length during the dry and rainy seasons, respectively.

Conversion of forest to cropland modifies the land surface characteristics affecting radiation budget and energy balance. For example, morphological changes in vegetation can change albedo, and physiological changes in vegetation can alter latent heat flux. A simulation study found that large-scale conversion of forest and grassland to cropland cools surface temperature by 0.7°C in summer and 1.1°C in winter in temperate latitudes, but warms surface temperature

by 0.8°C year-round in the tropics and subtropics (Bounoua et al. 2002). The temperature difference in response to deforestation between temperate latitudes and the tropics is mainly because of latent heat flux and the energy balance difference between the two regions. Our observed result on the change in surface air temperature owing to deforestation is within the range of the simulations by Bounoua et al. (2002). The 0.3°C difference in surface air temperature between our finding and the simulated results was probably because of difference in land cover perturbation and to the local meteorological condition (Zhao et al. 2001). Zhao et al. (2001) showed that temperature change caused by land cover changes affects only those regions where land cover was modified, but the effects can be propagated to remote regions after a short period. If this is true in the western Kenya highlands, we could anticipate that the ongoing rapid deforestation would continue to contribute to a small temperature increase in the region.

Significant correlations between average indoor temperature and gonotrophic cycle duration suggest that temperature is an important determinant of gonotrophic cycle length. That is, an increase of average indoor temperatures will lead to a reduction of the first and second gonotrophic cycle length, at least within the temperature range that we studied ($21\text{--}25^\circ\text{C}$). We observed that the second gonotrophic cycle length was considerably shorter than that of the first gonotrophic cycle. This is because females after the first bloodmeal have already developed ovaries to Christophers' stage 2 (Christophers 1949). Lyimo and Takken (1993) reported that small *A. gambiae* females tended to require two or three bloodmeals to complete the first gonotrophic cycle. In the current study we found 42.7–67.3% of the females successfully laid eggs after the first bloodmeal. It is unknown whether the females that did not lay eggs were smaller.

Using the mark-release-recapture method, Rodriguez et al. (1992) found the gonotrophic cycle of *Anopheles albimanus* Wiedemann to be 4 d for nulliparous mosquitoes and 2 d for parous mosquitoes in southern Mexico. Charlwood and Graves (1986) reported a gonotrophic cycle duration of 2.4–3.2 d for *Anopheles koliensis* Owen, 2.7–3.7 d for *Anopheles punctulatus* Donitz, and 2.1–3.0 d for *Anopheles farauti* Laveran in Papua New Guinea. Hii et al. (1990) observed a 2 to 3 d gonotrophic cycle duration in *Anopheles balabacensis* Biasas in Malaysia. Few such studies have been conducted in the Afrotropical anopheline mosquitoes, but our results on the gonotrophic cycle duration of *A. gambiae* by using confined cages are consistent with the studies on other mosquitoes. Negative correlation between gonotrophic cycle duration and temperature also has been reported in other mosquito species. For example, Mahmood and Crans (1997) reported that the amount of time required for bloodmeal digestion and oviposition decreased significantly with each increment in temperature from 10 to 28°C in *Culiseta melanura* Coquillett. Neto and Navarro-Silva (2004) exposed *Aedes albopictus* (Skuse) to different cyclic temperatures of $25/18^\circ\text{C}$

and 27/20°C and found that the gonotrophic cycle was shorter for the higher temperatures.

Our results have implications for considering the effect of land cover changes on malaria transmission in African highlands. Malaria transmission force may be measured by vectorial capacity. Vectorial capacity is defined as $ma^2p^n / (-\log_e p)$, where m is the relative density of vectors in relation to humans, a is mosquito daily biting frequency, p is the proportion of vectors surviving per day, and n is the duration of sporogony in days (MacDonald 1957). Mosquito biting frequency is inversely proportional to gonotrophic cycle length. At our study site, deforestation shortened the first gonotrophic cycle from 4.6 d to 2.9 d and from 10.1 d to 8.6 d during the dry and rainy seasons, respectively. This implies that deforestation would lead to an increase in the mosquito biting frequencies in the dry and rainy seasons in the highland. Because vectorial capacity is a function of a square of daily human-biting frequency, an increase in daily biting frequency would translate to an increase in vectorial capacity. Deforestation also has been shown to increase the survivorship of *A. gambiae* larvae and reduce the larva-to-adult developmental time in the highland (Tuno et al. 2005). The consequences of these factors acting together would be a dramatic increase in vectorial capacity. As human populations increase in the highlands of western Kenya and elsewhere in the East African regions, deforestation and its subsequent effects on malaria transmission will continue.

In summary, this study demonstrated that deforestation in the highlands increased the indoor temperatures where blood-fed *A. gambiae* reside. One consequence of indoor temperature increase is the shortening of the duration of the gonotrophic cycle and thus an increase in daily biting frequency and malaria transmission potential.

Acknowledgments

We thank L. Abala and R. Oriango for the technical help. Drs. G. Zhou and E. Mushinzimana assisted with data analysis. N. Minakawa, A. Demo, and two anonymous reviewers provided valuable comments on the manuscript. This study is published with the permission of the Director, Kenya Medical Research Institute. This work was supported by National Institutes of Health grants D43 TW01505 and R01 A150243.

References Cited

- Bouma, M. J. 2003. Methodological problems and amendments to demonstrate effects of temperature on the epidemiology of malaria. A new perspective on the highland epidemics in Madagascar, 1972–89. *Trans. R. Soc. Trop. Med. Hyg.* 97: 133–139.
- Bounoua, L., R. DeFries, G. J. Collatz, P. Sellers, and H. Khan. 2002. Effects of land cover conversion on surface climate. *Climatic Change* 52: 29–64.
- Brooks, T. M., S. L. Pimm, and J. O. Oyugi. 1999. Time lag between deforestation and bird extinction in tropical forest fragments. *Conserv. Biol.* 13: 1140–1150.
- Christophers, R. S. 1949. Endemic and epidemic prevalence, pp. 698–721, volume I. In M. Boyd [ed.], *Malariology*. Saunders, Philadelphia, PA.
- Charlwood, J. D., and P. M. Graves. 1986. Capture-recapture studies with mosquitoes of the group of *Anopheles punctulatus* Donitz (Diptera: Culicidae) from Papua New Guinea. *Bull. Entomol. Res.* 76: 211–227.
- [FAO] Food and Agriculture Organization. 1993. Forest resources assessment 1990. Tropical countries. FAO forestry paper no. 112. Food and Agriculture Organization, Rome, Italy.
- Githeko, A. K., and W. Ndegwa. 2001. Predicting malaria epidemics in the Kenya highlands using climate data: a tool for decision makers. *Global Change Hum. Health* 2: 54–63.
- Hay, S. I., A. M. Noor, M. Simba, M. Busolo, H. L. Guyatt, S. A. Ochola, and R. W. Snow. 2002. Clinical epidemiology of malaria in the highlands of western Kenya. *Emerg. Infect. Dis.* 8: 543–548.
- Hii, J. L., M. H. Birley, and V. Y. Sang. 1990. Estimation of survival rate and oviposition interval of *Anopheles balabacensis* mosquitoes from mark-recapture experiments in Sabah, Malaysia. *Med. Vet. Entomol.* 4: 135–140.
- Lindblade, K. A., E. D. Walker, A. W. Onapa, J. Katungu, and M. L. Wilson. 2000. Land use change alters malaria transmission parameters by modifying temperature in a highland area of Uganda. *Trop. Med. Int. Health* 5: 263–274.
- Lindsay, S. W., and W. J. Martens. 1998. Malaria in the African highlands: past, present and future. *Bull. World Health Organ.* 76: 33–45.
- Lyimo, E. O., and W. Takken. 1993. Effects of adult body size on fecundity and the pre-gravid rate of *Anopheles gambiae* females in Tanzania. *Med. Vet. Entomol.* 7: 328–332.
- MacDonald, G. 1957. The epidemiology and control of malaria. Oxford University Press, Oxford, England.
- Mahmood, F., and W. J. Crans. 1997. A thermal heat summation model to predict the duration of the gonotrophic cycle of *Culiseta melanura* in nature. *J. Am. Mosq. Control Assoc.* 13: 92–94.
- Manga, L., J. C. Toto, and P. Carnevale. 1995. Malaria vectors and transmission in an area deforested for a new international airport in southern Cameroon. *Ann. Soc. Belg. Med. Trop.* 75: 43–49.
- Matola, Y. G., G. B. White, and S.A. Magayuka. 1987. The changed pattern of malaria endemicity and transmission at Amani in the eastern Usambara mountains, north-eastern Tanzania. *J. Trop. Med. Hyg.* 90: 127–134.
- Minakawa, N., S. Munga, F. Atieli, E. Mushinzimana, G. Zhou, A. K. Githeko, and G. Yan. 2005. Spatial distribution of anopheline larval habitats in western Kenyan highlands: effects of land cover types and topography. *Am. J. Trop. Med. Hyg.* 73: 157–165.
- Neto, P. L., and M. A. Navarro-Silva. 2004. Development, longevity, gonotrophic cycle and oviposition of *Aedes albopictus* Skuse (Diptera: Culicidae) under cyclic temperatures. *Neotrop. Entomol.* 33: 29–33.
- Omar, S.A., I. S. Adagu, D.W. Gump, N. P. Ndaru, and D. C. Warhurst. 2001. *Plasmodium falciparum* in Kenya: high prevalence of drug-resistance-associated polymorphisms in hospital admissions with severe malaria in an epidemic area. *Ann. Trop. Med. Parasitol.* 95: 661–669.
- Rodriguez, M. H., D. N. Bown, J. I. Arredondo-Jimenez, C. Villarreal, E. G. Loyola, and C. E. Frederickson. 1992. Gonotrophic cycle and survivorship of *Anopheles albimanus* (Diptera: Culicidae) in southern Mexico. *J. Med. Entomol.* 29: 395–399.

- Round-Turner, D. [ed.]. 1994. Kakamega forest, the official guide. Kenya Indigenous Forest Conservation Programme, Nairobi, Kenya.
- SAS Institute. 1994. JMP® user's guide. SAS Institute, Cary, NC.
- Service, M. W., A. Voller, and D. E. Bedwell. 1986. The enzyme-linked immunosorbent assay (ELISA) test for the identification of blood-meals of haematophagous insects. *Bull. Entomol. Res.* 76: 321–330.
- Shanks, G. D., K. Biomndo, S. I. Hay, and R. W. Snow. 2000. Changing patterns of clinical malaria since 1965 among a tea estate population located in the Kenyan highlands. *Trans. R. Soc. Trop. Med. Hyg.* 94: 253–255.
- Some, E. S. 1994. Effects and control of highland malaria epidemic in Uasin Gishu District, Kenya. *East Afr. Med. J.* 71: 1–8.
- Tuno, N., W. Okeka, N. Minakawa, M. Takagi, and G. Yan. 2005. Survivorship of *Anopheles gambiae* sensu stricto (Diptera: Culicidae) larvae in western Kenya highland forest. *J. Med. Entomol.* 42: 270–277.
- Walsh, J. F., D. H. Molyneux, and M. H. Birley. 1993. Deforestation: effects on vector-borne disease. *Parasitology* 106: S55–S75.
- Zhao, M., A. J. Pitman, and T. N. Chase. 2001. Climatic effects of land cover change at different carbon dioxide levels. *Climate Res.* 17: 1–18.
- Zhou, G., N. Minakawa, A. K. Githeko, and G. Yan. 2004. Association between climate variability and malaria epidemics in the East African highlands. *Proc. Natl. Acad. Sci. U.S.A.* 101: 2375–2380.

Received 29 March 2005; accepted 20 July 2005.
