Modeling the Spatio-Temporal Distribution of the *Anopheles* Mosquito based on Life History and Surface Water Conditions

Momoyo Kashiwada and Shunji Ohta*

Department of Human Behavior and Environment Sciences, Faculty of Human Sciences, Waseda University, 2-579-15 Mikajima, Tokorozawa, Saitama 359-1192, Japan

Abstract: To describe the temporal and geographic distribution of the malaria vector mosquito (*Anopheles*) at a fine resolution, we modeled the relationship between mosquito life history and climate conditions, focusing on temperature-dependent development of the mosquito. Because *Anopheles* has aquatic immature life stages, the model was designed to incorporate information on surface moisture conditions suitable for the mosquito. Development was estimated using either air or water temperature, depending on the developmental stage. The model was able to predict seasonal patterns of occurrence of *Anopheles* at representative sites with reasonable accuracy. Individual emergence of mosquitoes was limited by low water temperatures and/or low moisture conditions at the soil surface in cold or dry seasons. This model was then applied to obtain the geographic distribution of *Anopheles* occurrence in Monsoon Asia. Spatio-temporal emergence of the *Anopheles* mosquito was successfully represented using the model and simple climate data. This model can be used to predict the distribution of the mosquito for malaria risk assessments under future scenarios involving climate change and the effects of El Niño-Southern Oscillation events.

Keywords: Climatic conditions, life history, malaria, temperature-dependent development, spatio-temporal distribution, water bucket model, water temperature model.

INTRODUCTION

Because malaria is a mosquito-borne disease, occurrence data for the vector mosquito *Anopheles* are needed for malaria risk assessments. Martens *et al.* (1999) assessed the risk of malaria transmission based on the geographic distribution of this mosquito species by country or administrative unit (WHO 1989, Jetten & Takken 1994). However, the mosquito is not always uniformly distributed within a country, and its range typically crosses national borders. Most entomological studies are unable to incorporate a detailed distribution of the vector mosquito species, although it is the basis for risk assessment of malaria transmission, because the number of observation sites of the *Anopheles* mosquito is small. Thus, model predictions of *Anopheles* distribution are necessary to enhance the present data for the distribution of the mosquito.

An integrated, process-based model for estimating the "transmission or epidemic potential" index of the vector population (Martens *et al.* 1999, van Lieshout *et al.* 2004) improved on other approaches by taking into account the female mosquito density and associated favorable climate conditions. This index approach is very useful for determining the risk of malaria transmission in a community where mosquito observations have not been conducted. However, climate conditions suitable for the adult female mosquito are not always those that are optimal for the immature stages of the mosquito. According to Bayoh & Lindsay (2003), the optimal temperature range for *Anopheles* development narrows as the mosquito develops. Furthermore, immature stages of *Anopheles* live in water such as puddles, pools, or streams; thus, it is necessary to consider the water temperature range suitable for the growth and development of the mosquito.

Recent studies mapping vector species have attempted to explain the geographic distribution of *Anopheles* and *Aedes* mosquitoes by analyzing climate variables for the mosquito observation sites using niche-based distribution models (Foley *et al.* 2008, Medley 2010) or a fuzzy logic model (Craig *et al.* 1999). These studies have generated high-resolution maps of the vectors over large spatial scales using climate data, and the maps are a good indicator of the present distribution of the vector. However, it is difficult for these maps to represent the temporal occurrence of the vectors, because the calculation time-steps in these studies were typically at least a month. However, mosquito development and the life cycle of immature life stages occur at time scales of several days to a few weeks.

On the other hand, ecophysiological approaches have been employed to explain the temporal occurrence of insects by describing their life histories. These models have calculated development with air temperature at each developmental stage of the insect, based on the assumption that the growth of an insect is dependent on the temperature of its habitat (Hopp & Foley 2001, Depinay *et al.* 2004). Although such ecophysiological models can generally explain the temporal population dynamics of pest insects at a specific site, they were not able to estimate the geographical distribution of the *Anopheles* mosquito (Depinay *et al.*

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*Address correspondence to this author at the Department of Human Behavior and Environment Sciences, Faculty of Human Sciences, Waseda University, 2-579-15 Mikajima, Tokorozawa, Saitama 359-1192, Japan; Tel: +81-4-2947-6903; Fax: +81-4-2947-6903; E-mail: shun@waseda.jp

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developmental time than the other stages. It is clear that the developmental rate (day^{-1}) increases with temperature (Fig. **2**). We determined the lower temperature threshold as 15 °C, because, according to the previous experiments, mosquitoes could not develop into adult below this temperature (Bayoh & Lindsay 2003; Depinay *et al.* 2004). The plotted data were fitted using the linear least-squares method and the resulting regression equations were used to calculate the daily developmental rate (R_{Temp}) using Eq. (1).

Adaptation of the Growth Model to an Ideal Site for the Mosquito

Immature mosquito development takes place in small water bodies such as puddles or other artificial water containers. To consider the potential distribution of the *Anopheles* mosquito, the availability of a natural water surface was assumed in this study. Under natural conditions, these would be small pools in marsh or wetland areas with some plant cover. For this study, the *Anopheles* mosquito was assumed to develop in a small body of water with an area of a few square meters. To exclude areas that were too arid for an immature mosquito to survive, the soil moisture content was taken into account. Soil moisture content at the depth of plant roots was calculated using the water budget approach proposed by Hopp & Foley (2001) and Tao *et al.* (2003). Calculation of the soil moisture content on the *i*th day (W_i) was conducted using the following equation:

$$W_i = \min (W_{i-1} + P_i + M_i - AE_i, W^*) \quad (4)$$

where W_{i-1} is the soil moisture content at the end of the previous day (i - 1), P_i is the daily precipitation (mm d^{-1}), M_i is the daily snow melt on the *i*th day, AE_i is the actual evapotranspiration on the *i*th day, and W^* is the soil moisture holding capacity, which reflects the effects of soil texture, soil organic content, and plant root depth, obtained from Dunne & Willmott (1996). Tao *et al.* (2003) determined the value of AE_i as a ratio of the available moisture content to the potential evapotranspiration (PE_i) calculated using the FAO Penman-Monteith method (Allen *et al.* 1998). This method assumes PE_i for cropland; coefficients prior to cultivation were derived from Allen *et al.* (1998), because an immature mosquito was assumed to live in a small pool in natural areas such as wetlands or marshes. Calculation of PE_i requires data for net radiation, air temperature, air humidity, and wind speed. In the present study, net radiation was calculated using an energy balance equation (Ohta *et al.* 1993), and wind speed was assumed to be constant at 2 ms^{-1}, in accordance with Allen *et al.* (1998).

Temperature of the Water Body in which the Mosquito Lives

The temperature of the water body in which the *Anopheles* mosquito lives directly affects immature mosquito development. Unfortunately, water temperature has not been measured with fine resolution spatially and temporally, as has been done for both air temperature and precipitation. According to Ohta & Kimura (2007), the water temperature in temperate regions is lower than the air temperature by 2-4°C during the period of insufficient net radiation in the winter. Conversely, the water temperature is higher than the air temperature by 1-2 °C in the spring. Because these seasonal changes in the differences between air and water temperatures are complex, it cannot be assumed that air temperature and water temperature are the same.

Ohta *et al.* (1993) evaluated the temperature of ponded shallow water with a water depth of 5-10 cm without percolation or heat flux due to irrigation, and modeled water temperature as initially affected by energy partitioning between air, water, and soil. This modeled condition is nearly the same as the ideal habitat for the immature stages of the mosquito considered in this study. Therefore, water temperature was estimated using a simple energy balance model, as well as the methods developed by Ohta *et al.* (1993). Calculation of the water temperature requires basic climate factors, including air temperature, solar radiation, cloud cover, and vapor pressure.

Data Used for Calculation of the Temporal and Spatial Distributions

Climate Data Used for Application of the Model

Data for the Asian region (70-150° E, 10° S-50° N) were used in the model (Fig. **3**). All climate data had a spatial resolution of 0.5° lat × 0.5° long (about 50 km^2, total number of grid cells = 19481), interpolated or extrapolated climatologically or geologically if necessary. The CRU Global Climate Dataset, available through the IPCC Data Distribution Center (New *et al.* 1999) was used for the model calculations. Monthly data for air temperature, precipitation, vapor pressure, solar radiation, and cloud cover were included in the dataset for 1961-1990 climate normals. If daily data were not available for the model, monthly values were converted to daily data using cubic spline or linear interpolations, ensuring consistency of the daily values with monthly means or totals. Although it is desirable to obtain daily climate data for model calculation, these interpolation methods enabled us to perform the calculation when only the monthly values of air temperature, precipitation, vapor pressure, solar radiation, and cloud cover were available.

Mosquito Observation Data Used for Validation of the Model

For validation of the model, we gathered observation data for the *Anopheles* mosquito from the literature (Fig. **3**). Observation data for the entire year were available only for Yunnan Province in China (Ono 1992), Ishigaki Island in Japan (Toma *et al.* 2002), Kyonggi-do in South Korea (Lee *et al.* 2002), Cheolwon and Yeoncheon Counties in South Korea (Yeom *et al.* 2005), Chiang Mai in Thailand (Overgaard *et al.* 2002), Kheda District in India (Konradsen *et al.* 1998), and Assam in India (Dev 1996).

Yunnan (a rural community at 21.75° N, 100.75° E, altitude 500 m) is located in southwest China, bordering three malaria-endemic countries, Myanmar, Laos, and Vietnam. Ishigaki Island (24.30° N, 124.10° E, altitude 6 m) is located approximately 700 km south of Okinawa Island. Malaria was endemic on Ishigaki Island and the other islands of Yaeyama, Ryukyu Archipelago until 1962. Kyonggi-do (37.50° N, 127.25° E, altitude 85 m) is a northern county bordering North Korea. These border regions suffer from infiltration of infected mosquitoes from North Korea from June to September. Cheolwon (38.14° N, 127.31° E, altitude 0 m) and Yeoncheon (38.09° N, 127.07° E, altitude 0 m) are

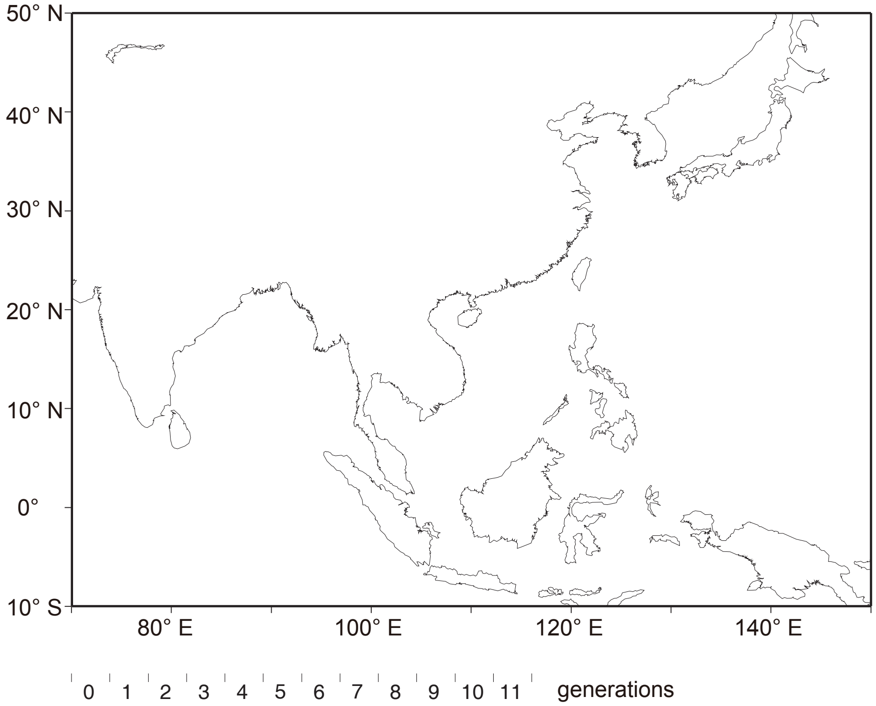

Fig. (8). Geographic distribution of the maximum number of generations.

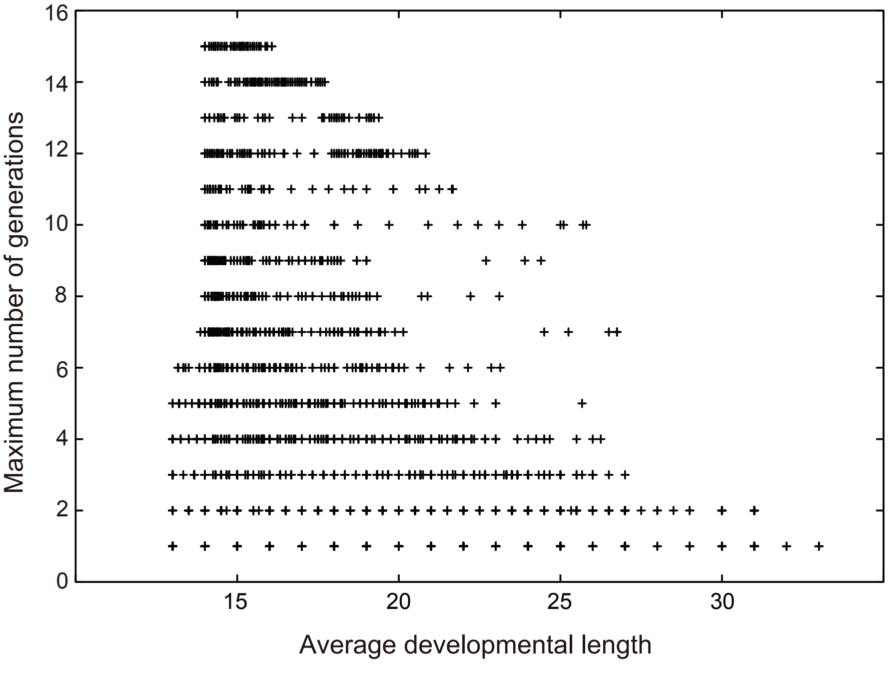

Fig. (9). Relationship between the average duration of *Anopheles* mosquito development and the maximum number of generations.

as the average developmental length ($D_{average}$) decreases. However, some plots in Fig. (**9**) have low values for G_{max}, despite low values for $D_{average}$. The relationship between average developmental length and the maximum number of generations is not well correlated (R = -0.337).

Latitudinal Variation in Climate Conditions

The habitat of the mosquito was limited by soil moisture content and water temperature (Figs. **6** and **8**). The duration of adult mosquito occurrence, optimal moisture conditions, and optimal temperatures for transects A, B, and C (Fig. **3**) are shown in Fig. (**10**) to analyze the limiting factors for mosquito growth. In Fig. (**10**) (upper panel), the periods in which the maximum developmental stage was > 3 are illustrated as vertical bars, indicating potential adult mosquito emergence. The center and lower panels of Fig. (**10**) show the duration of optimal moisture conditions and water temperatures for the mosquito, respectively.

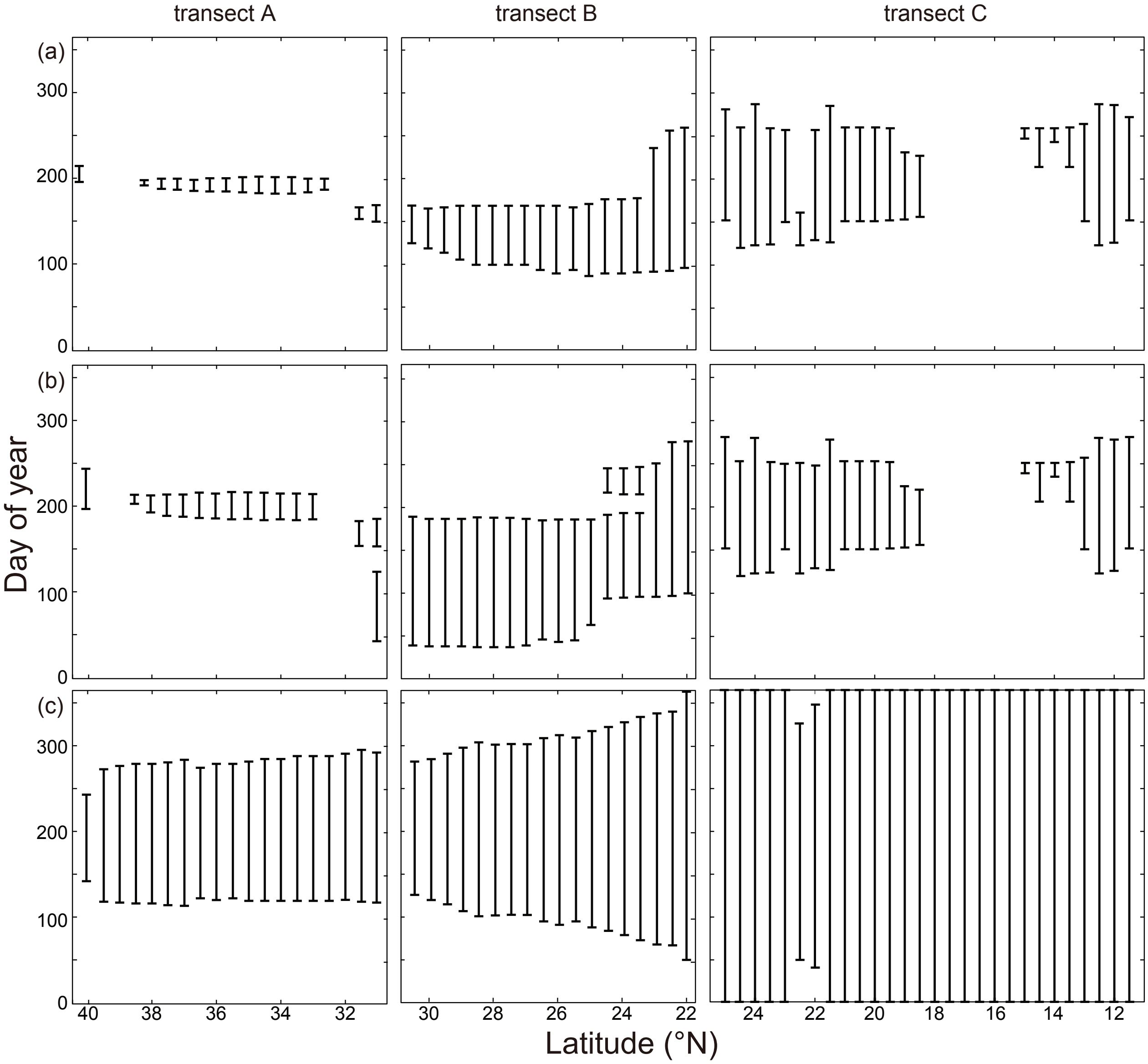

Fig. (10). Latitudinal variations in the occurrence of the *Anopheles* mosquito and its limiting factors along transects shown in Fig. (**3**): (**a**) periods of adult mosquito occurrence, (**b**) periods of optimal moisture conditions, (**c**) periods of optimal temperatures. The bottom of the bar indicates the start date of the period and the top of the bar indicates the end of the period.

The duration of the adult stage at latitudes above 33° N along transect A (corresponding to eastern China) was limited to < 50 d, although the duration of optimal water temperatures was approximately 150-200 d in the same region. There were also gaps in the periods of optimal water temperature and optimal moisture content along transect B, corresponding to southeastern China. However, these gaps in the optimal conditions were not as wide as for transect A (middle and lower panels of transects **A** and **B** in Fig. **10**). The longest period of adult emergence occurred at latitudes below 13° N and at 18-24° N along transect C in Cambodia and Bangladesh, where the durations of both the optimal temperature and optimal moisture conditions were longest. Although the water temperature was suitable for mosquito growth throughout the year along transect C, the duration of the adult stage was limited due to a shortage of moisture from 16-18° N, corresponding to northwestern Thailand.

DISCUSSION

Characteristics of the Model for the Potential Distribution of *Anopheles*

The results of the life history model (central panels in Fig. **5**) for the temporal occurrence of the *Anopheles* mosquito coincided with the observations of occurrence at each intensive observation site, which represented various climates such as humid tropical, semi-arid, and temperate regions (lower panels in Fig. **5**). The model was not able to simulate the temporal variations in mosquito occurrence (Fig. **4**) as accurately as the results of Depinay *et al.* (2004), likely because they focused on a local site. Simulation of the seasonal changes in mosquito occurrence was sufficient to evaluate potential occurrence on a broad scale. The model accurately simulated the geographic distribution, and the distribution obtained from the model show trends similar to that of the mosquito observations (small closed circles in Fig. **3**) and the results of Hopp & Foley (2001), who simulated the geographic distribution of the *Aedes* mosquito. The niche-based (Foley *et al.* 2008, Medley 2010) and fuzzy logic (Craig *et al.* 1999) models based on calculations with a time-step of one year were able to show only annual average distributions for the mosquito. The present model is able to illustrate the seasonal changes in the geographic distribution of the mosquito by calculating mosquito growth with a time-step of one day (Fig. **6**). The results obtained from the model are not actual but potential distribution of the *Anopheles* mosquito.

Remarks on the Temporal and Spatial Distributions of *Anopheles* in Asia

This method was developed to express the temporal and spatial distributions of the *Anopheles* mosquito in Asia. There are three main conclusions that can be drawn from the results.

First, the distribution and the duration of appearance of the *Anopheles* mosquito were limited by soil moisture content rather than water temperatures (Figs. **9** and **10**). The lack of correlation between the average developmental length and the maximum number of generations shown in Fig. (**9**) indicates that the duration of *Anopheles* appearance is limited by insufficient moisture conditions. It is seldom that both optimal water temperature and soil moisture conditions exist simultaneously in many areas of inland Asia, such as eastern China and northwestern Thailand (Fig. **10**). Although the developmental length of the *Anopheles* mosquito in Eastern China (transect A) is relatively short compared to that at the same latitudes (Fig. **7**), the growing period is severely limited to approximately 50 d due to reduced soil moisture content (Fig. **10**).

Second, the geographic distribution of the *Anopheles* mosquito based on our results (Figs. **6** and **8**) differs from that of malaria transmission (WHO 1989, Jetten & Takken 1994, Martens *et al.* 1999). It is possible for temperate regions such as the southernmost part of Japan to have mosquitoes in the summer, as these regions are within the potential climatological distribution area of the *Anopheles* mosquito, although malaria has been completely eradicated. The maximum number of generations is not large enough to support malaria transmission in temperate regions (Fig. **8**).

Third, the model results indicated that the duration of mosquito emergence and distribution is climatically limited to a few rainy months in semi-arid areas, such as inland India, where the malaria incidence is very high at the present time (Figs. **6** and **8**). The malaria incidence in India has been reported throughout the country (WHO 2008) and the model results for this area underestimated the current distribution. This may be caused by the lack of developmental rate data for the species that are found in India (Fig. **2**). Similar variance in the climatologically based distribution of the vector mosquito and actual distribution was also reported by Hopp & Foley (2001), and the study noted that people living in dry regions tend to store water in and around their homes, providing ample breeding grounds for this domestic species (Shope 1991). Furthermore, irrigation canal water or other agricultural water use has also been identified as a habitat for vector production in semi-arid areas (Konradsen *et al.* 1998). To estimate mosquito occurrence in such cases, the model should incorporate not only water movement in the vertical direction, such as precipitation and evapotranspiration, but also in the horizontal direction, such as human water use.

Necessity for Experimental and Observational Data

Although this study provides a framework for assessment of the *Anopheles* mosquito distribution in relation to climate factors, basic data on mosquito biology is limited. In particular, experimental data on the relationship between temperature and developmental rate of the mosquito is limited (Fig. **2**); thus, it was necessary to include data for various *Anopheles* mosquito species of Asia and Africa. To simulate the mosquito population dynamics at local sites, data for each species are needed. Observations of the seasonal variations in the *Anopheles* population used to validate the model were limited to only eight sites. To better assess the transmission risk of malaria for a variety of cases, it is recommended that such data from a variety of field studies around the world be developed and shared (Hay *et al.* 2009).

Application of the Model to Changing Climate Conditions

Most studies that have assessed the impacts of climate change on the incidence and geographical range of malaria have assumed that the mosquito distribution would not change under future climate conditions (Martens *et al.* 1999, van Lieshout *et al.* 2004). The present model will contribute to evaluation of the effects of future climate change on malaria transmission through assessment of the potential future distribution of the *Anopheles* mosquito.

The present model, driven by simple climate data, is able to predict the basic distribution of the mosquito to assess the transmission risk of malaria and changes under climate change scenarios such as El Niño-Southern Oscillation (ENSO). ENSO events cause rainfall patterns to change, and this typically affects the habitat of immature stages of the vector mosquito. Rainfall in arid regions and drought in humid climates create pools that are suitable for mosquito development (Kovats *et al.* 2003). Although the relationship between ENSO and malaria incidence has been quantified (Kovats *et al.* 2003, Mabaso *et al.* 2007), analysis of this relationship focusing on vector mosquito occurrence has not been conducted. To elucidate the effects of ENSO on epidemic malaria, mosquito occurrence can be simulated using the model developed in this study.

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