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Original Contribution

Assessment of the Impact of Climate Shifts on Malaria Transmission in the Sahel

Arne Bomblies[1] and Elfatih A. B. Eltahir[2]

[1]*University of Vermont, 221 Votey Hall, 33 Colchester Ave., Burlington, VT*
[2]*Parsons Laboratory, Massachusetts Institute of Technology, Room 48-207, 15 Vassar St., Cambridge, MA 02139*

Abstract: Climate affects malaria transmission through a complex network of causative pathways. We seek to evaluate the impact of hypothetical climate change scenarios on malaria transmission in the Sahel by using a novel mechanistic, high spatial- and temporal-resolution coupled hydrology and agent-based entomology model. The hydrology model component resolves individual precipitation events and individual breeding pools. The impact of future potential climate shifts on the representative Sahel village of Banizoumbou, Niger, is estimated by forcing the model of Banizoumbou environment with meteorological data from two locations along the north–south climatological gradient observed in the Sahel—both for warmer, drier scenarios from the north and cooler, wetter scenarios from the south. These shifts in climate represent hypothetical but historically realistic climate change scenarios. For Banizoumbou climatic conditions (latitude 13.54 N), a shift toward cooler, wetter conditions may dramatically increase mosquito abundance; however, our modeling results indicate that the increased malaria transmissibility is not simply proportional to the precipitation increase. The cooler, wetter conditions increase the length of the sporogonic cycle, dampening a large vectorial capacity increase otherwise brought about by increased mosquito survival and greater overall abundance. Furthermore, simulations varying rainfall event frequency demonstrate the importance of precipitation patterns, rather than simply average or time-integrated precipitation, as a controlling factor of these dynamics. Modeling results suggest that in addition to changes in temperature and total precipitation, changes in rainfall patterns are very important to predict changes in disease susceptibility resulting from climate shifts. The combined effect of these climate-shift–induced perturbations can be represented with the aid of a detailed mechanistic model.

Keywords: malaria, climate change, hydrology, anopheles mosquitoes, agent-based modeling

INTRODUCTION

Malaria transmission is partially controlled by environmental conditions, and environmental variability may largely explain spatial and temporal variability in malaria transmission intensity. This is partly because the *Anopheles* mosquitoes responsible for malaria transmission depend on surface water availability for breeding habitat. Favorable precipitation patterns and land surface hydrology allow these breeding habitats to form and persist. Strong temperature dependencies of parasite and vector development

Correspondence to: Arne Bomblies, e-mail: abomblie@uvm.edu

rates and vector mortality also influence malaria endemicity (Craig et al., 1999; Depinay et al., 2004; Martens, 1997). Therefore, significant social and economic influences on malaria notwithstanding, climate variability presents a dominant control of malaria transmission variability. An understanding of the nature of malaria transmissibility response to climate variability can enhance the prediction of epidemics and the effects of longer-term climate change. In this paper, we explore the linkage of malaria transmission with climate in the West African Sahel, using a validated, mechanistic mathematical model, HYDREMATS (HYDRology Entomology and MAlaria Transmission Simulator; Bomblies et al., 2008).

In some regions, such as desert fringe environments, the availability of suitable breeding pools limits mosquito abundance. Temperature also influences malaria transmission through temperature-dependent larval, egg, and parasite development rates, as well as mosquito longevity (Depinay et al., 2004). Increased temperature results in faster development of eggs within the mosquito, parasite within the mosquito (extrinsic incubation), and larval stages. However, subadult (larval-stage) mosquitoes suffer thermal death beyond a threshold temperature of 40°C (Jepson et al., 1947). In addition, adult mosquito longevity is reduced with increasing temperatures (Martens, 1997). Consequently, in regions where the average temperature is sufficiently low or sufficiently high, parasite development time within the mosquito (extrinsic incubation period) exceeds the average lifespan of the mosquito, clearly preventing endemic malaria in these areas (Craig et al., 1999). This temperature limitation defines boundaries of endemic zones, which are further restricted by hydrologic suitability for breeding habitat formation and microclimates (Thomson et al., 2004). Areas outside of these malaria-conducive regions are free of sustained, endemic malaria transmission. However, these areas may experience periodic epidemics as climatic conditions temporarily shift to favor malaria transmission (Kiszewski and Teklehaimenot, 2004). Such a shift in climate conditions may include temperature fluctuations affecting development rates, or rainfall pattern changes resulting in altered mosquito breeding habitat availability.

In the Sahel of West Africa, a strong north–south rainfall gradient separates the Sahara desert from the wet equatorial forests near the Atlantic coast. The Sahel is roughly bracketed by the 200-mm isohyet to the north and the 600-mm isohyet to the south over only a few hundred kilometers (Fig. 1). Within this zone, the rainfall gradient is approximately 1 mm km^{-1} (Lebel et al., 1992). Northward migration of the Intertropical Convergence Zone (ITCZ) during the West African monsoon (May–October) is responsible for virtually all of the rainfall in this region, but the annual maximum northward extent of the thunderstorm belt associated with this seasonal pattern displays

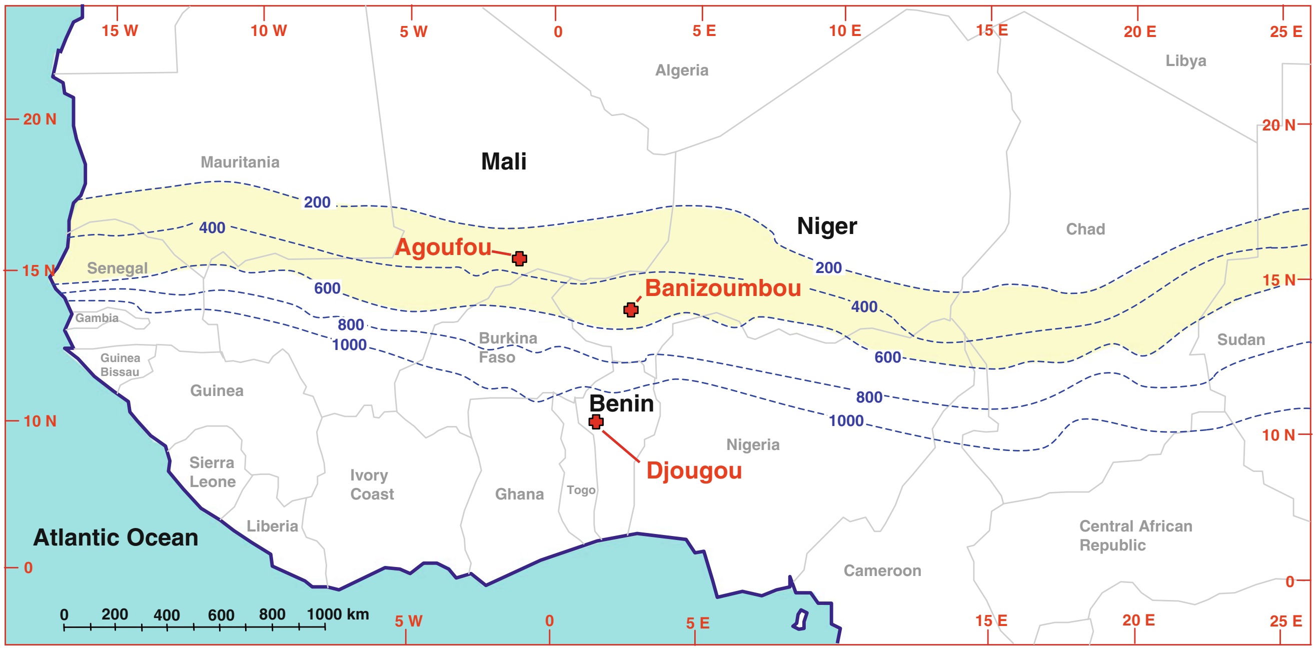

Figure 1. Locations of Banizoumbou, Niger; Agoufou, Mali; and Djougou, Benin, and rainfall gradient of the sahel. Isohyets are labeled with annual average millimeters of rain.

high interannual variability, largely driven by fluctuations in sea surface temperature in the Atlantic Ocean (Lamb, 1978; Giannini et al., 2003). The impact of this interannual climate variability on human populations is perhaps most evident by its effect on agricultural activity in the Sahel. Individual years of below-average rainfall have resulted in devastating famines, most recently in 2005 in Niger, which was primarily caused by very low precipitation during the 2004 monsoon.

Climate and ecological conditions in the Sahara desert and the Sahel occasionally undergo dramatic shifts from dry to wet regimes and vice versa (Wang and Eltahir, 2000; Claussen, 1998). Three notable examples of such "regime changes" in the Sahel climate have drastically altered climate patterns and affected vegetation and rainfall. The first occurred approximately 6,000 years ago during the middle Holocene. This shift caused an abrupt 500-km northward movement of rainfall contours as well as associated vegetation (Irizarry-Ortiz et al., 2003; Hoelzmann et al., 1998). After this shift, approximately 5,500 years ago, a sudden transition from wet to dry conditions occurred in the Sahel, and the last example involved the onset of a persistent, multi-decadal drought beginning in the late 1960s (Foley et al., 2003). All three of these climate shifts have translated isohyets along the precipitation gradient and have demonstrated remarkable persistence. The magnitudes of the changes that caused past climate shifts were probably very similar to those observed occasionally in modern times (Nicholson, 2000). Therefore, such climate shifts constitute the climatological basis for our analysis. For a specific site in the Sahel and for a specific period, a good representation of potential climate conditions arising from shifts to dry (respectively wet) conditions may be the concurrent conditions found north (respectively south) of the site for the same period. For a specific period, two locations along the north–south rainfall gradient would exhibit climate differences comparable to those of two different climate regimes at a stationary site. Therefore, we assume that effects of drastic climate shifts on malaria transmission can be studied by comparing model results forced by climate data sets from various locations along the Sahelian north–south climatological gradient.

MATERIALS AND METHODS

In this paper, we explore the effects of climate variability on Sahel malaria transmission using the Hydrology, Entomology, and Malaria Transmission Simulator (HYDREMATS) of Bomblies et al. (2008), which consists of a distributed hydrology model coupled to an agent-based entomology and malaria transmission model. This model was designed to represent the formation and persistence of the typical rain-fed pools, which allow the breeding of *Anopheles gambiae* mosquitoes, and individually represent mosquitoes as they interact with their natural and human environments. Characteristics relevant to malaria transmission are tracked for each mosquito and human. Model inputs are precipitation, temperature, humidity, radiation, and wind speed and wind direction time series. Corresponding output is water depths for each hourly time step of the simulation for each rectangular model grid cell, and mosquito abundance.

HYDREMATS forms a mechanistic modeling link between climatic forcing and the resulting entomological response (for which hydrology is a necessary intermediate) and gets around limitations of correlative approaches linking environmental conditions to malaria. The model facilitates highly detailed studies of population response to various perturbations. The hydrology component of the model incorporates distributed soil and vegetation types to simulate rainfall-runoff transformation, infiltration, and overland flow toward topographically low points. With this spatially explicit structure, applied at high spatial and temporal resolution, HYDREMATS can predict entomological response to rainfall of variable intensity, frequency, and duration and accounts for antecedent moisture conditions. This is a powerful capability for understanding malaria response to rainfall in environments of water-limited mosquito population dynamics, such as the Sahel.

As discussed in the study by Bomblies et al. (2008), HYDREMATS has been field validated using 2 years of intensive hydrological and entomological field observations in southwestern Niger. In this study, we apply HYDREMATS to the location of these field observations (Banizoumbou, Niger; Fig. 1) and assume that the model calibration is valid for all of the scenarios presented.

Representation of Climate Variability

We assume that climate shifts in the Sahel can be represented as a seasonal north–south translation of isohyets and isotherms. For a certain location in the Sahel, climatic conditions in dry periods resemble typical climatic conditions for locations further north. Conversely, for the same location, the climatic conditions in wet periods would resemble the typical climate conditions of locations further south. Meteorological station data records were taken from the African Monsoon Multidisciplinary Analyses (AMMA) project database, for two sites—Djougou, Benin, and Agoufou, Mali (Fig. 1)—represent wet and dry shifts, respectively. These were used to compare with model results from simulations using in situ meteorological data recorded at a station directly in Banizoumbou.

The Banizoumbou weather station (13.53° N, 2.66° E) was installed by ORSTOM (present-day IRD, Institute de Rechereche pour le Développement) of France and has been collecting data for several years during the AMMA project, beginning in 2004. Long-term precipitation climatology, however, is better considered at nearby Niamey because of a much longer record. During the period 1905–1989, the average annual rainfall in Niamey was 562 mm (Le Barbé and Lebel, 1997). Rainfall occurs only during the May–September monsoon, which peaks in August. Extended drought during the period 1968–1990 decreased the average annual precipitation to 495 mm (Le Barbé and Lebel, 1997). Average annual rainfall in recent years in Banizoumbou is slightly less at 450 mm. For simulation purposes, we use Banizoumbou meteorological data.

Djougou is a large market town in north-west Benin (9.705° N, 1.667° E), at 430 meters elevation. Average rainfall in Djougou was 1258 mm during the 25-year period 1978–2003 (Weller, 2003). Rainfall records in Djougou and Banizoumbou display a significant difference, as a result of the steep rainfall gradient in the Sahel. Djougou is located 420 km south of Banizoumbou in the north–south direction, along the precipitation gradient. In contrast, Agoufou, Mali is located at 15.34° N, 1.48° W, and is 197 km north of Banizoumbou in the north–south direction along the precipitation gradient. Agoufou is still within the Sahel bioclimatic zone; however, the long-term average annual rainfall is only 370 mm (Baup et al., 2007). Agoufou is at an elevation of approximately 310 meters above sea level (Baup et al., 2007). Table 1 summarizes variations in the climate data for the three sites.

D'Amato and Lebel (1998) found that inter-annual rainfall variability in the Niger Sahel depends primarily on the number of precipitation events per rainy season. The weak correlation of individual event magnitude with annual rainfall is not statistically significant, suggesting that the primary mode of inter-annual rainfall variability is event frequency instead of magnitude (D'Amato and Lebel, 1998). Because hydrologic response to rainfall events depends strongly on antecedent moisture conditions, rainfall frequency may play a major role in pool persistence. If soil and pools have sufficient time to dry out between rain events, impacts of the subsequent rainfall on ponding will be diminished because of higher infiltration and lower runoff. To assess the contribution of rainfall frequency to variability in mosquito abundance, we isolated the effects of rainfall frequency by scaling 2006 Agoufou and Djougou precipitation series to Banizoumbou 2006 seasonal total rainfall (478 mm). In one of our simulation scenarios, this new, synthetic precipitation series is applied to the Banizoumbou environment. Temperature, humidity, and seasonal total rainfall distribution remain unchanged in this scenario. The number of rainfall events registered at the three measurement sites in 2006, the average interstorm period, and the average event rainfall are summarized in Table 1.

Table 1. Summary of 2005 and 2006 Climatic Differences at Banizoumbou, Niger; Agoufou, Mali; and Djougou, Benin

	Banizoumbou, Niger	Agoufou, Mali	Djougou, Benin
Altitude (masl)	250	290	454
Latitude	13.54° N	15.30° N	9.69° N
Longitude	2.67° E	1.48° W	1.66° E
2005 precipitation (mm)	405	153.7[a]	1325
2006 precipitation (mm)	478	345.3	951
2005 monsoon Temp (°C)	28.6	29.0	25.1
2006 monsoon Temp (°C)	29.1	30.83	26.0
2005 relative humidity	44%[a]	46.6%	71.9%
2006 relative humidity	61.4%	49.9%	71.6%
2006 average days between events	2.6	2.5	1.45
2006 number of events	48	54	126
2006 average event rainfall	10.0	7.0	7.5

[a] Some data are missing.

Temperature and relative humidity vary among these three sites as well. During the 2006 wet season, the Banizoumbou meteorological station registered an average temperature of 29.1°C and an average relative humidity of 61.4% for the 5-month period, May–September. In Djougou, average temperature and relative humidity for the same period were 26°C and 71.6%, respectively, and in Agoufou, the same variables were 30.8°C and 49.9%, respectively. Agoufou, Mali has slightly warmer and drier conditions than Banizoumbou, and as expected Djougou, Benin is cooler and more humid. Temperature variability also is more pronounced in Agoufou. These variables are summarized in Table 1.

Hydrology

For a detailed description of HYDREMATS, see Bomblies et al. (2008). The model represents land surface hydrology at high spatial and temporal resolution, to yield hourly predictions of pooled water formation and persistence at 10-meter spatial scale. The model borrows heavily from the Land Surface Transfer model LSX (Pollard and Thompson, 1995). Following LSX, the model simulates two vegetation layers and six soil layers, but applies the water, energy, and momentum calculations at a high resolution for the small model domain sizes. Cell-to-cell overland flow has been added. The model simulates runoff generation from each grid cell in the model domain, with distributed land surface characteristics (vegetation type, soil type, Manning's roughness) determining runoff. This runoff is then routed over the infiltrating land surface into the topographic low points using an implicit finite difference solution of the overland flow equations. Temperature, humidity, and solar radiation influence the transpiration and soil evaporation rates, and thus influence soil moisture. Soil moisture in turn influences energy partitioning into latent and sensible heat, which affects soil temperatures, and finally soil temperatures influence soil evaporation as well as the temperature of runoff arriving in topographic low points. Water temperatures in ponded areas are thus simulated and are used in the entomology model to determine the subadult (aquatic-stages: egg, larva, pupa) mosquito growth rates within individual pools.

Aquatic Stage Entomology

Each model grid cell predicted to contain pooled water is capable of hosting subadult mosquitoes. The presence of subadults depends on an individual gravid female mosquito laying a clutch of eggs in the pool, as well as constant persistence of pooled water. A compartmental model simulates the temperature-dependent advancement of mosquito larvae from one stage to the next, with intraspecific competition simulated with an assigned carrying capacity regulating advancement rates. Pupae mature into emergent adult mosquitoes, which enter the model domain as independent individuals free to interact with their environment.

Vectorial Capacity

Vectorial capacity is a variable that represents the daily rate of infective bites received by a single human host. Vectorial capacity can be interpreted as malaria transmissibility, because it relates characteristics of the mosquito vector population (such as abundance and daily survival probability) to potential disease spread, without information about actual parasite presence within the population. The expression for vectorial capacity is:

$$C = \frac{ma^2p^n}{-\ln(p)} \tag{1}$$

where m = abundance term (mosquitoes per human); a = number of blood meals per vector per day; P = daily survival probability of vectors (0–1); n = extrinsic incubation period of parasite in days.

Environmental conditions affect the abundance term, which depends on breeding habitat persistence, the daily survivability term, which depends on daily average temperatures, and the extrinsic incubation period (development time of parasite within the mosquito) for which Detinova (1962) noted a degree-day dependence on temperature.

The a variable in Equation 1 representing the number of blood meals per vector per day results from an average number of mosquito/human agent interactions representing blood meals within the entomology model component. This is updated for each time step.

Mosquito Mortality

Mosquito mortality depends on daily average temperature, according to Martens (1997). High temperatures stress the mosquitoes, and thereby decrease the daily survival probability. A decrease in the expected daily survival probability of individuals results in a population-scale decrease in mosquito abundance, and also diminishes the fraction of infected mosquitoes surviving the extrinsic incubation period. The combination of these effects makes temperature-determined mosquito mortality a highly consequential variable for malaria transmission. The Martens model is reproduced here:

$$p = \exp\left(\frac{-1}{-4.4 + 1.31T - 0.03T^2}\right) \tag{2}$$

where P = daily survival probability (0–1); T = daily average temperature (°C).

Sporogonic Cycle

The sporogonic cycle length (n in Equation 1) represents the time required for development of infectious sporozoites within the mosquito salivary gland. Once sporozoites are fully developed, the mosquito becomes infectious and transmission can occur. Detinova (1962) reported that 111 degree-days $>16°C$ are necessary for *Plasmodium falciparum* sporozoite development, resulting in the following representation:

$$n = \frac{111}{T - 16} \tag{3}$$

where n is the length of time in days for sporozoite development, and T is the ambient temperature in degrees C. The asymptotic rise at 16°C clearly indicates that malaria incubation at this temperature and below is impossible, and that near 16°C, incubation period far exceeds the typical mosquito lifespan of several weeks.

Climatological limitations of malaria transmission have been previously modeled by Craig et al. (1999). Using Equations 1–3, they define limits of areas in Africa suitable to *Plasmodium falciparum* malaria transmission based on the temperature-limited development of mosquitoes and malaria parasite within the mosquito midgut. To explore the effects of climate shifts in the Sahel on malaria transmission, we employ the same models (Equations 1–3) describing temperature limitations on biological development. However, our mechanistic hydrology modeling approach adds an additional dimension to this problem. HYDREMATS allows the prediction of breeding pool response to consistent changes in precipitation and temperature that typically accompany climate shifts. More accurate prediction of changes in mosquito abundance (m) following climate shifts should be possible with this approach.

RESULTS

Several simulations were performed to evaluate the effects of climate variability on mosquito population dynamics. These included simulations to assess the impact of climate shifts, the impact of temperature shifts taken alone, and the impact of shifts in precipitation patterns.

Impact of Climate Shifts

Meteorological data from Djougou, Benin was applied to Banizoumbou to evaluate the effects of more humid, higher-precipitation conditions typical of several hundred kilometers south of Banizoumbou. Meteorological data measured during the 2006 monsoon was applied to the same model grid as the baseline simulation in Banizoumbou. Similarly, precipitation, temperature, humidity, and solar radiation data recorded at the Agoufou, Mali meteorological station were applied to the Banizoumbou model domain to gauge the effects of hotter, drier conditions. The cumulative mosquito abundances for these variable climate forcings are presented in Fig. 2. Clearly, mosquito abundance responds strongly to the favorable meteorological conditions of Djougou, Benin. Cumulative abundance increases by 127% if meteorological conditions of Djougou are applied to Banizoumbou and decreases 34% if the drier, hotter conditions of Agoufou are applied. Maximum abundance increases by 52% for the Djougou meteorological data, and decreases by 25% for the Agoufou station data. Finally, Fig. 3 presents the simulated vectorial capacity for the climate shift scenarios. Maximum vectorial capacity in the wetter, cooler Djougou climate conditions increased by 25% relative to the 2006 Banizoumbou baseline. In contrast, maximum vectorial capacity decreased by 26% for the drier, warmer Agoufou, Mali scenario with respect to the Banizoumbou baseline scenario. For the Djougou, Benin scenario, the increase of vectorial capacity is lower than the increase of mosquito abundance because of the temperature dependence of sporogony. Days required for sporozoite generation (n term in Equation 1) increases dramatically at lower temperatures, reducing vectorial capacity. At the lower temperatures typical of

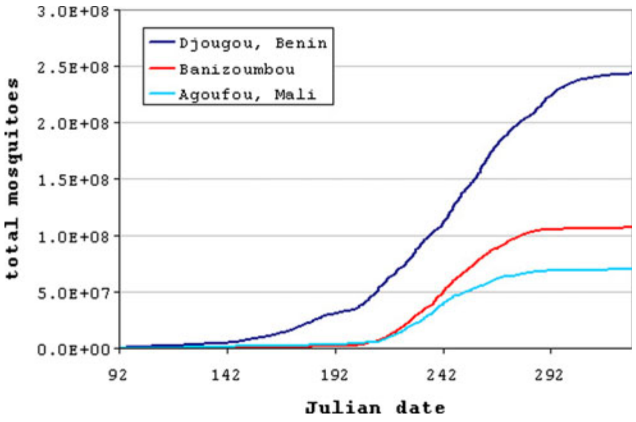

Figure 2. Cumulative simulated mosquitoes, for all meteorological station data from Agoufou, Mali and Djougou, Benin applied to Banizoumbou. Baseline, unperturbed Banizoumbou climate output is included.

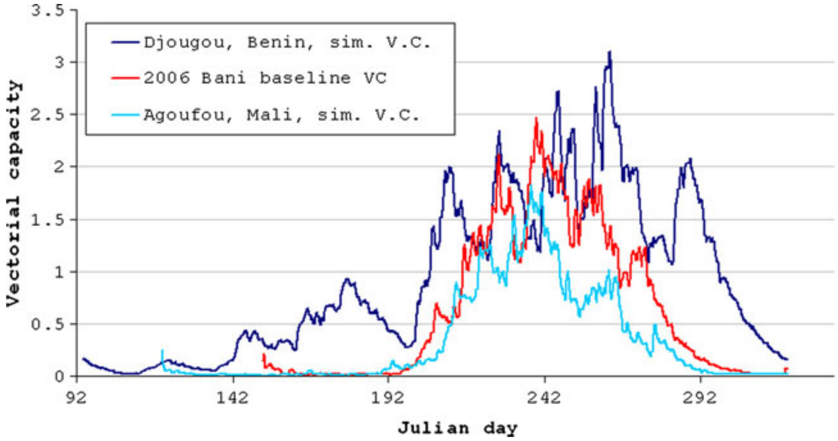

Figure 3. Simulated vectorial capacities for all meteorological station data from Agoufou, Mali and Djougou, Benin applied to Banizoumbou.

Djougou, Benin, the temperature dependence of daily survivability is not very strong (Martens, 1997).

Impact of Shifts in Temperature

The effects of individual climate variables were determined by isolating them in several test scenarios. First, only Djougou (Benin) temperature was applied to the Banizoumbou environment, holding precipitation and other meteorological variables (wind speed, wind direction, and solar radiation) constant. The same was then done for Agoufou temperature. Maximum abundance increased by 9% when the cooler Djougou, Benin temperatures were applied to Banizoumbou and decreased by 24% using the warmer temperature series from Agoufou, Mali. Simulated cumulative mosquito abundances are shown in Fig. 4. In this case, Djougou temperatures resulted in a 16% increase in cumulative mosquitoes compared with a 22% decrease in cumulative mosquitoes using Agoufou temperatures. The simulated temperature effects on abundance do not include the potential dampening effect of mosquitoes seeking shelter in cooler microclimates, such as houses or the shade of tree canopies. A mosquito may fly to such a location in extreme heat and rest. This behavior would lessen the effects of high temperatures.

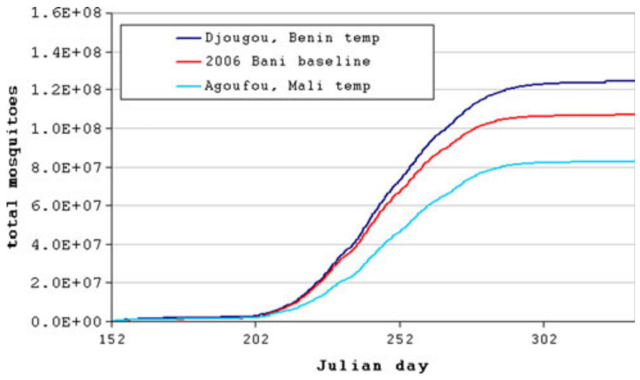

Figure 4. Cumulative simulated mosquitoes applying only Agoufou, Mali and Djougou, Benin records to the baseline simulation.

From Table 1, 2006 average temperatures in Agoufou were only 0.7° warmer than Banizoumbou compared with a 3.3° difference between Banizoumbou and Djougou temperatures. The pronounced temperature-dependent daily survivability of the Martens (1997) model (Equation 2) is responsible for this drastic decrease using the warmer Agoufou temperatures. The daily survivability decreases much more rapidly at higher temperatures, which occasionally occur in this part of Mali, than at more moderate temperatures typical of Banizoumbou and Djougou, Benin. Fig. 5 shows a histogram of 24-hour average temperatures calculated using Djougou, Agoufou and Banizoumbou temperature series. The few 24-hour average temperature events shown in Fig. 5 that are >38°C cause the daily survival to decrease to approximately 60% in Agoufou compared with the relatively constant 90% daily survival between 16°C and 32°C. The simulation operates at an hourly time step, but simulated mosquitoes respond to daily average temperature. Hourly mosquito survivability is derived from the daily survivability, which is calculated using Equation 2 with the average temperature of the previous 24 h. The minor increase in abundance resulting from higher subadult development rate at elevated temperatures is overshadowed by the effect of decreased survivability. Due to the dominant influence of average temperature on survivability, climate conditions of Agoufou, Mali, largely control abundance by temperature-decreased longevity, for at least part of the transmission season.

The effects of higher temperatures on vectorial capacity are more pronounced than the elevated-temperature effects

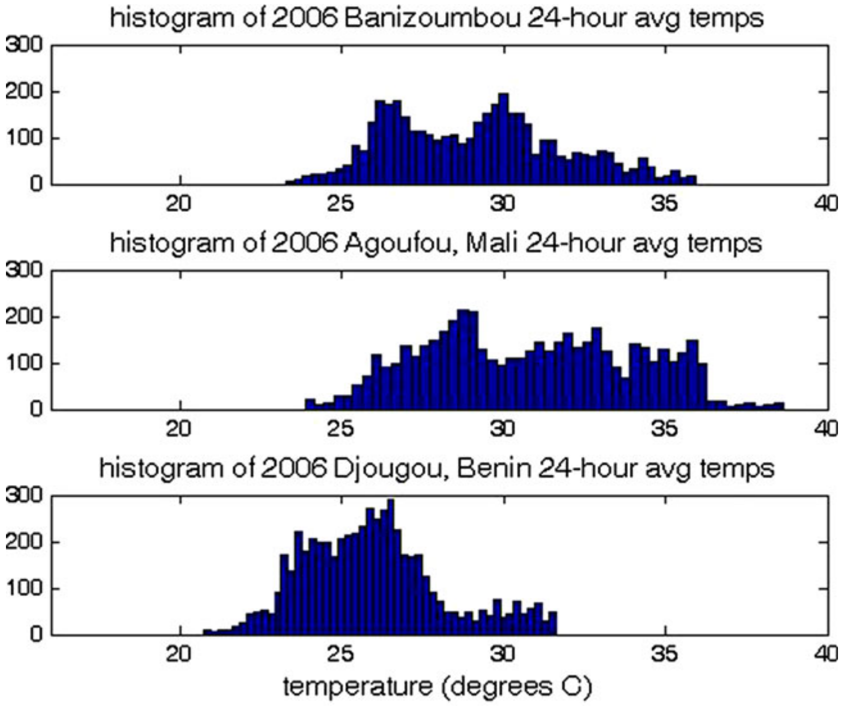

Figure 5. Histograms showing daily average temperature distributions for 2006 temperature records (May–October).

on abundance alone, due to the nonlinear dependence of vectorial capacity on daily survivability and the temperature dependence of extrinsic incubation period *n*. Maximum vectorial capacity for this temperature variation experiment is shown in Fig. 6. Maximum predicted vectorial capacity decreases for both scenarios. Agoufou temperatures caused a 28% decrease in maximum vectorial capacity, whereas Djougou temperatures caused a 13% decrease in maximum vectorial capacity. Here, the temperature dependence of sporogony becomes evident once again. Similar to the high 24-hour average temperatures exhibited by the Agoufou temperature record, Fig. 5 shows several days of daily average temperatures <23°C in Djougou. At these temperatures, sporogony advances slowly, and the durations often exceed mosquito lifespans. At low temperatures, sporozoite development time *n* (Equation 3) becomes large rapidly as temperature decreases compared with the much less pronounced variation of *n* at temperatures >25°C. This low sporozoite development rate is the reason vectorial capacity decreases in Djougou relative to Banizoumbou, despite the increase in mosquito abundance. The minor effect on vectorial capacity of increased longevity at lower temperatures is overshadowed by the effects of increased *n*, because the longevity dependence is not very steep at these temperatures.

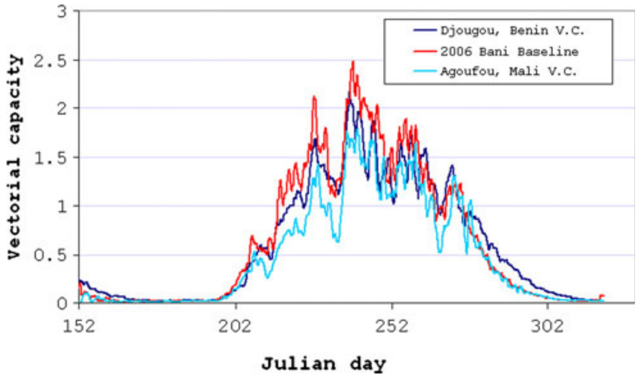

Figure 6. Simulated vectorial capacity trends, applying only Agoufou, Mali and Djougou, Benin temperature records to the Banizoumbou baseline simulation.

Impact of Shifts in Precipitation Patterns

Precipitation affects pool formation and persistence not only by total amount, but also by event frequency. Average interstorm periods during the 2006 monsoon vary from 1.45 days in Djougou to 2.5 days in Agoufou and 2.6 days in Banizoumbou (Table 1). Higher frequency of rainfall events is expected to keep pools more consistently filled; however, a high frequency of low rainfall events may not be sufficient for maintaining productive breeding habitats. We evaluated the effects of frequency by scaling Agoufou and Djougou rainfall series to Banizoumbou total precipitation such that all three precipitation series sum to 478 mm, which is the 2006 Banizoumbou total precipitation. In this way, effects of variations in precipitation frequency were isolated while keeping total seasonal precipitation constant. Temperature series were left unchanged from the Banizoumbou baseline conditions. The results for mosquito abundance and cumulative mosquitoes for this scenario are presented in Figs. 7 and 8, respectively. In this experiment, maximum abundance increased by 11% when Agoufou, Mali scaled precipitation was applied to Banizoumbou and decreased by 24% when Djougou, Benin scaled precipitation was applied to Banizoumbou. Cumulative simulated mosquitoes were increased by 8% using the Agoufou synthetic scaled precipitation record and decreased 38% using the Djougou precipitation. Because Djougou, Benin experienced more precipitation events during 2006 than Agoufou, Mali, the scaling process reduced the magnitude of each event in Djougou and raised the magnitude of each event in Agoufou to result in the total of 478 mm of rainfall recorded in Banizoumbou.

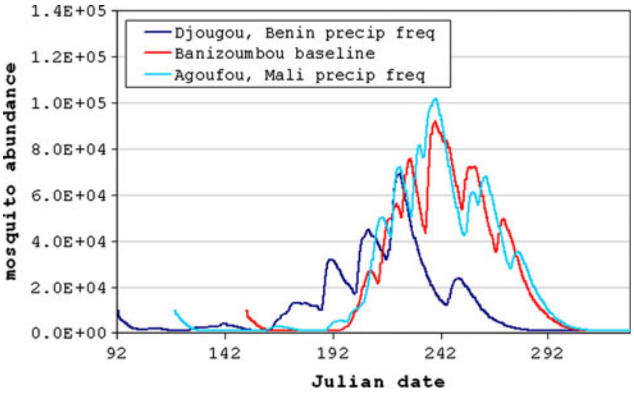

Figure 7. Simulated mosquito abundance using scaled precipitation records from Agoufou, Mali and Djougou, Benin applied to Banizoumbou. Total seasonal precipitation equals that of Banizoumbou, but storm frequency varies.

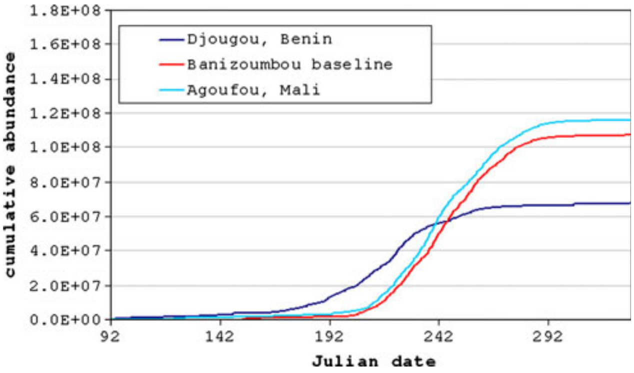

Figure 8. Cumulative simulated mosquitoes using scaled precipitation records from Agoufou, Mali and Djougou, Benin applied to Banizoumbou.

The results from this scenario demonstrate the controls of local hydrologic response to rainfall on mosquito population dynamics. HYDREMATS assumes that subadult (aquatic-stage) mosquitoes die if their breeding pool dries out before they emerge as adult mosquitoes. Therefore, any pool desiccation results in a reduction of abundance by killing a cohort of developing subadult mosquitoes. Soil and vegetation types influence the infiltration losses from a pool, and partitioning of rainfall into infiltration and runoff depends strongly on soil moisture. Soil moisture responds to precipitation events, the frequency of which can determine emergence or death for aquatic-stage mosquitoes. Water depths of a large, highly productive pool in the center of Banizoumbou are presented in Fig. 9, for the synthetic precipitation series of Agoufou, Mali (top) and Djougou, Benin (bottom). The frequent drying-out events in the Djougou scenario contrast markedly to the uninterrupted periods of water in the pool in the case of Agoufou precipitation applied to Banizoumbou. Due to this hydrologically determined pool persistence, the synthetic Agoufou precipitation series allows more adult mosquito emergence, resulting in the higher overall mosquito abundance for this scenario, despite the later start of mosquito breeding evident in Fig. 8. Thus, the importance of precipitation frequency and distribution through the wet season becomes evident. Vectorial capacity differences are not presented because only the abundance term of the vectorial capacity is changed as a result of the scaled precipitation series. The temperature series recorded at the Banizoumbou station is used in all simulations. Percent changes in maximum vectorial capacities are therefore identical to the percent changes in maximum abundance.

DISCUSSION

We have used a very high-resolution, mechanistic modeling tool to simulate malaria transmission response to climate shifts in one specific village: Banizoumbou, Niger. Banizoumbou is a very specific environment. Certainly the configuration of various soil types and topography dictating pool locations at Banizoumbou is unique, but nevertheless it is instructive to note the strong controls that hydrologic processes exhibit on the abundance term of the

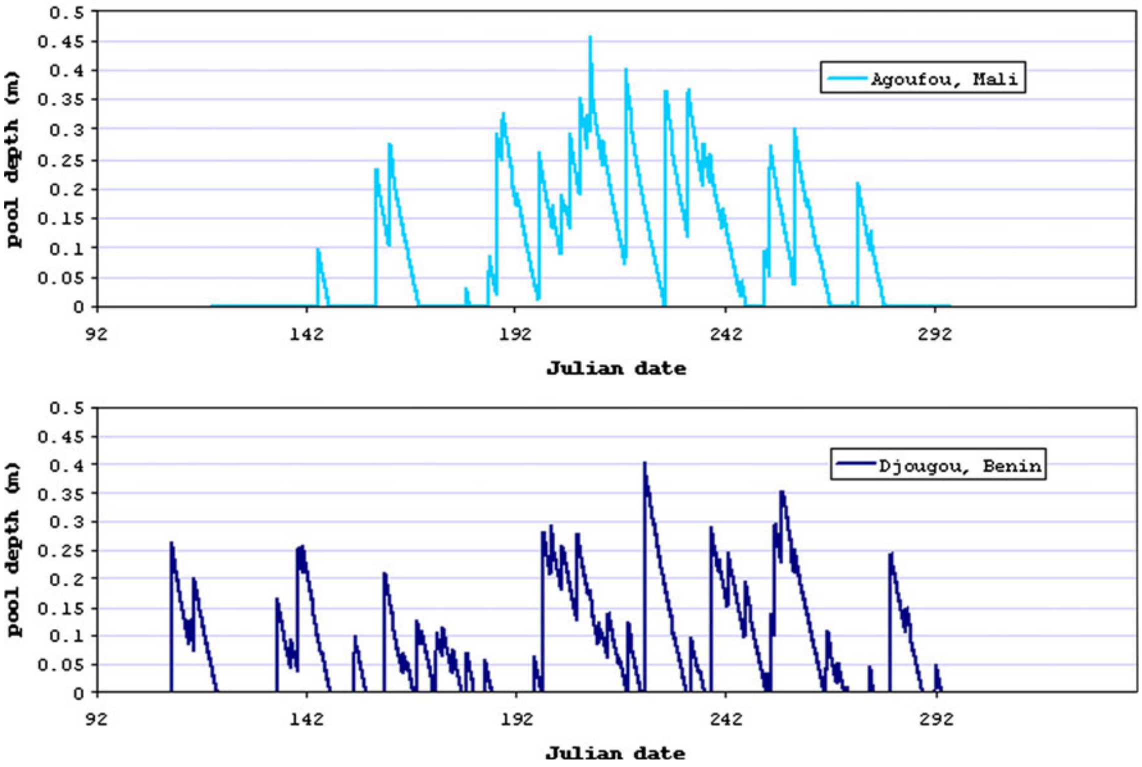

Figure 9. Water depths at a dominant pool in the center of Banizoumbou, for the scaled precipitation series from Agoufou, Mali (*top*) and Djougou, Benin (*bottom*) applied to the Banizoumbou model domain.

vectorial capacity equation. Mosquito populations respond favorably to long periods of uninterrupted pool persistence, because many cohorts of subadult mosquitoes can emerge without suffering fatal desiccation. Dry pools are assumed to result in complete sterilization, based on field observations (Bomblies et al., 2008). We have demonstrated how manipulations of rainfall series to alter the frequency and number of events—while maintaining the same total annual precipitation—can lead to dramatic differences in pool persistence and therefore mosquito abundance. Because the number of rainfall events and the event frequency often are the primary manifestations of precipitation variability in the Sahel, the implications of such precipitation changes resulting from climate shifts on malaria transmission becomes evident. Increased event frequency associated with a shift to wetter conditions will increase abundance more than a simple linear correlation with rainfall would suggest, and for decreased event frequency the opposite is true because of more frequent pool dry-outs. The general dependence of mosquito abundance on small-scale hydrology will be common to all water-limited villages in the Sahel, in which the dominant malaria vectors breed in ephemeral rain-fed pools.

Modeling results also reveal that the temperature changes that accompany climate shifts can limit malaria transmission by slowing the development of parasite or decreasing the survival probability of mosquitoes, depending on whether the shift is to wetter or drier conditions. Not all temperature changes associated with future climate shifts will necessarily involve temperature limitations in malaria transmission, and the various causative pathways linking temperature and malaria transmission would have different relative magnitudes depending on average temperatures attained during the climate shift and resulting diurnal temperature extremes. These include aquatic stage development rate (increase with temperature), survival (decrease with temperature), sporogonic cycle (increase with temperature), and the number of influences on hydrology, which are relatively minor (e.g., evapotranspiration rates).

Two nonlinear processes determine conditions necessary for malaria transmission to occur: pool persistence must exceed mosquito development time, and mosquito lifespan must exceed parasite extrinsic incubation period. Due to the complexity of the many environmental causations (primarily precipitation and temperature) leading to malaria transmission, it is difficult to predict impacts of changes without resorting to numerical models. Even though HYDREMATS embodies all of the important environmentally influenced processes that affect malaria transmission, a few potential changes are not simulated. First, the longer-term vegetation changes that result from and provide positive feedback for Sahel climate shifts may affect local hydrology enough to alter pool persistence and influence runoff volume entering topographic low points. As previously discussed, persistence of pools is a dominant control of mosquito abundance in the Sahel. Partitioning of incident rainfall into runoff and infiltration and surface roughness will change in response to changes in vegetation cover. These processes will affect pond formation, and roughness length of the vegetation cover will affect transpiration rates. Moreover, vegetation changes resulting from climate shifts will provide positive feedbacks to the climate shifts. Second, human populations are very adaptable and will adjust to changes in climate. In the model experiments, we assume a static human population. Most Sahel inhabitants are subsistence farmers, who would be forced to adapt to climate shifts to grow enough food to survive. Such social influences are not considered and may affect malaria transmission.

Model results are presented in terms of changes in abundance and vectorial capacity resulting from climate shifts. Vectorial capacity is a useful indicator of malaria transmissibility. However, changes in vectorial capacity do not generally translate to equivalent changes in malaria prevalence, particularly in high-transmission environments. For example, the Garki Project conducted in northern Nigeria revealed that a 90% reduction in vectorial capacity resulted only in a 25% reduction in malaria prevalence (Molineux and Gramicci, 1980). In other regions of Africa, higher vector abundance resulting from expanded irrigation schemes in areas of stable transmission has been associated with lower malaria prevalence, an observation termed the "paddies paradox" (Ijumba and Lindsay, 2001; Mutero et al., 2004). The lack of a direct vectorial capacity/prevalence correlation results from a multitude of factors, which can be environmental, ecological, or physiological. These factors can all play a role in the complex relationship of entomological activity and vectorial capacity to disease manifestations. Nevertheless, to assess climate-driven variability of disease susceptibility in a certain area, vectorial capacity remains a useful measure.

CONCLUSIONS

Model results highlight the complexity of malaria response to climate shifts and demonstrate the model's ability to isolate the sensitivity of this complex system to individual climate variables, such as temperature and precipitation. Based on the results of several simulations, we conclude that generalized predictions of malaria response to climate change should be made very cautiously and that careful study of specific scenarios with the aid of detailed models is necessary for achieving credible predictions.

Taken together, modeling results indicate various modes of control on malaria transmissibility in terms of vectorial capacity, which may result from climate shifts in the Sahel. Changes in rainfall patterns and precipitation frequency associated with climatic shifts affect mosquito abundance nonlinearly, due to small-scale hydrologic processes that influence pool persistence resulting from a particular rainfall pattern. To illustrate this, we have demonstrated that Agoufou, Mali and Djougou, Benin 2006 hourly rainfall series scaled to the 2006 Banizoumbou rainfall total have resulted in significantly different simulated mosquito abundances. This is due to the importance of persistent pools for uninterrupted breeding of successive mosquito cohorts. Previous models' predictions of mosquito abundance using time-integrated results of total rainfall fail to consider individual rainfall event frequency as a control of drying-out events of individual pools, and the model results presented in this study demonstrate this deficiency. Rainfall frequency and event magnitude are important variables because they influence the timing of pool formation and persistence. In addition, precipitation event frequency is the dominant mode of variability in Sahel precipitation, suggesting that a detailed modeling approach as presented in this paper is appropriate to predict the impacts of future changes on malaria transmission in the Sahel.

A shift toward cooler, wetter conditions, such as the drastic shift of 6,000 years ago in the Sahara may dramatically increase mosquito abundance; however, our modeling results indicate that the increased malaria transmissibility is not simply proportional to the precipitation increase. The cooler, wetter conditions increase the length of the sporogonic cycle, dampening a large vectorial capacity increase otherwise brought about by increased mosquito survival and greater overall abundance. In contrast, a shift to hotter, drier conditions results in much lower daily survival probability for adult mosquitoes leading to drastically lower vectorial capacity. Decreased abundance that stems from fewer newly formed breeding pools compounds this reduction in malaria transmissibility. Therefore, strong climate shifts in either direction may limit malaria transmission by different biological limitation mechanisms. Due to the complexity of the climate/hydrology/disease transmission system, climate shifts may affect vectorial capacity in a number of ways that are impossible to predict without the use of mechanistic predictive models, such as HYDREMATS.

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