Int J Biometeorol
DOI 10.1007/s00484-012-0630-y

ORIGINAL PAPER

Effect of irrigation systems on temporal distribution of malaria vectors in semi-arid regions

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Received: 9 April 2012 / Revised: 17 December 2012 / Accepted: 25 December 2012

Abstract Previous research models have used climate data to explain habitat conditions of *Anopheles* mosquitoes transmitting malaria parasites. Although they can estimate mosquito populations with sufficient accuracy in many areas, observational data show that there is a tendency to underestimate the active growth and reproduction period of mosquitoes in semi-arid agricultural regions. In this study, a new, modified model that includes irrigation as a factor was developed to predict the active growing period of mosquitoes more precisely than the base model for ecophysiological and climatological distribution of mosquito generations (ECD-mg). Five sites with complete sets of observational data were selected in semi-arid regions of India for the comparison. The active growing period of mosquitoes determined from the modified ECD-mg model that incorporated the irrigation factor was in agreement with the observational data, whereas the active growing period was underestimated by the previous ECD-mg model that did not incorporate irrigation. This suggests that anthropogenic changes in the water supply due to extensive irrigation can encourage the growth of *Anopheles* mosquitoes through the alteration of the natural water balance in their habitat. In addition, it was found that the irrigation systems not only enable the active growth of mosquitoes in dry seasons but also play an important role in stabilizing the growth in rainy seasons. Consequently, the irrigation systems could lengthen the annual growing period of *Anopheles* mosquitoes and increase the maximum generation number of mosquitoes in semi-arid subtropical regions.

Electronic supplementary material The online version of this article (doi:10.1007/s00484-012-0630-y) contains supplementary material, which is available to authorized users.

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Keywords Anopheles · Growing period · Growth model · Irrigation · Water balance

Introduction

According to a recent report (WHO 2010), malaria is a serious infection that leads to more than 800,000 deaths and more than 200 million cases annually in the world today. Malaria infection occurs worldwide, but mainly in low latitudinal regions of Africa, Asia, and Central and South America. Because the *Anopheles* mosquito is the only insect species transmitting malaria, in order to estimate the risk of malaria infection it is essential that we accurately predict the potential for development of *Anopheles* mosquitoes. Previous malaria risk models showed that climate change will have an important impact on the length of the transmission season in many areas and described the transmission of malarial parasites from *Anopheles* to humans on the basis of climatic data (Martens et al. 1999; Lieshout et al. 2004). Since there has been an ecological succession of vector species in some areas because of climatic changes, there is a need to study the changing pattern of the vector distribution (Martens et al. 1999; Kearney et al. 2009; Ohta and Kaga 2011). Thus, we have developed a new model coupled with the ecophysiological and climatological distribution of mosquito generations (ECD-mg), which can describe ecophysiological growth of the *Anopheles* mosquitoes using simple climate factors (Ohta and Kaga 2012). Our model was applied to estimate the potential period of mosquito activity and their maximum generations per year in Asia (Ohta and Kaga 2012).

The ECD-mg model could express successfully the spatio-temporal distribution of *Anopheles* mosquitoes in Asia across the humid tropical to cool-temperate regions over a broad scale. However, the seasonal distribution of mosquitoes in semi-arid regions cannot be expressed using the ECD-mg model and other models (Martens et al. 1999; Lieshout et al. 2004). For example, the ECD-mg model has predicted that the temporal distribution of mosquitoes in the western part of India was limited to approximately the 3-month rainy season (Ohta and Kaga 2012). However, mosquitoes were observed in the same region also during the dry season (Kant and Pandey 1999; Rowland et al. 2000; Singh et al. 2004), and malaria infections have occurred throughout the year (Jayaraman 1982; Tyagi and Yadav 2001; Gupta et al. 2009). The annual number of infections in the same region reached more than 200,000 people in 1998 (Lal et al. 2000), corresponding to the total number of patients in Thailand (Chareonviriyaphap et al. 2000). From these studies, it can be concluded that the ECD-mg model had underestimated the temporal distribution of mosquitoes in semi-arid regions based on the observed infections.

Konradsen et al. (1998) propounded that the presence of *Anopheles* mosquitoes and malaria during the dry season was caused by agricultural irrigation in areas without sufficient soil water content. Because *Anopheles* have been observed frequently in the vicinity of artificially placed irrigation water, this strongly suggests that large amounts of irrigation water play the same function as precipitation and, consequently, led to the increase in *Anopheles* in the dry season (Kant and Pandey 1999; Herrel et al. 2001; Hytteborn 2005). In addition, Baeza et al. (2011) revealed that there is a positive correlation between the amount of irrigation water and malarial cases in Western India. Although the ECD-mg model was able to predict seasonal patterns of the occurrence of *Anopheles* under natural conditions (i.e., without irrigation) in the Assam and Kheda districts with a reasonable degree of accuracy (Ohta and Kaga 2012), it is necessary to modify the ECD-mg model to predict seasonal patterns of *Anopheles* under artificial conditions (i.e., with irrigation).

The first purpose of this study was to modify the ECD-mg model to incorporate the presence of irrigation water using data from crop calendars. Then, the modified ECD-mg was applied to correlate the data with the active period of the *Anopheles* mosquito that has been observed in semi-arid regions. Finally, the simulation results obtained can be used to provide insight into the effect of irrigation systems on the growth and distribution of *Anopheles* mosquitoes in these regions.

Materials and methods

Study sites and observational data on mosquitoes

Four major species of mosquitoes are found in semi-arid regions in India: *Anopheles culicifacies*, *A. subpictus*, *A. stephensi*, and *A. annularis*. In particular, *A. culicifacies* is the primary malaria vector in this area (e.g., Mahmood et al. 1984). The seasonal and spatial distributions of these species are different because of species-specific ecological and environmental factors. *A. stephensi* is found in urban areas and does not usually breed in agricultural fields. *A. subpictus* prefers open ground pools with little vegetation and is not present in winter. *A. culicifacies* prefers clean water including agricultural fields and *A. annularis* prefers clean water with abundant vegetation, especially paddy fields, ponds, and swamps.

In order to study the seasonal variations of *Anopheles*, it is necessary to observe *Anopheles* populations continuously for more than 1 year. Moreover, study sites must be chosen from semi-arid regions that are extensively irrigated and have a confirmed high prevalence of malarial infection. All observational data on *Anopheles* mosquitoes used in our model were collated from previously published information in semi-arid regions. In fact, five studies (Bhatt et al. 1991; Singh and Mishra 2000; Tyagi and Yadav 2001; Herrel et al. 2004; Joshi et al. 2005) have met our requirements by compiling continuous data observed on the population density and appearance time.

Agriculture occurred often, and irrigation periods were long at the five study sites. Bahawalnagar district [29.62° N, 73.13° E, 150 m above sea level (a.s.l.)] is located in South Punjab, Pakistan bordering the state of Rajasthan in India (Herrel et al. 2004), where annual precipitation is very low (120 mm) compared to other study sites (800–1,500 mm). At three villages located along the irrigation canal, collections were dominated by *A. subpictus* and *A. stephensi*, and to a lesser extent, *A. culicifacies*. Jaisalmer A (27.43° N, 71.92° E, 165 m a.s.l.) is located near the main Indira Gandhi canal in northwestern Rajasthan, India (Tyagi and Yadav 2001). Over the past few decades, water from the canal to this site in the Thar Desert has raised the water table and increased the water retention characteristics of the soil. This has allowed cultivation of rice and water-demanding crops that were not previously cultivable in the desert. In villages near the irrigated areas, three species (*A. culicifacies*, *A. stephensi* and *A. subpictus*) were mainly captured, although, in general, *A. stephensi* rarely lives in agricultural land. Jaisalmer B (26.38° N, 72.50° E, 280 m a.s.l.) is located in the central Thar Desert (Joshi et al. 2005). This area is characterized by extreme temperatures, large diurnal temperature ranges, and the lowest relative humidity throughout the year. The minimum temperature reached 1–2 °C in winter (January) with a maximum temperature of 45 °C in summer (April–June). In this irrigated area, four species (*A. subpictus*, *A. stephensi*, *A. culicifacies* and *A. annularis*) were collected. Kheda (22.74° N, 72.68° E, 15 m a.s.l.) is located northeast of the Gujarat state (Bhatt et al. 1991). The villages in this area are surrounded by a network of irrigation distributaries and drainage systems. Jabalpur (23.07° N, 79.71° E, 390 m a.s.l.) is located in Madhya Pradesh, central India (Singh and Mishra 2000), and contained a total irrigated area of

868 ha. In this irrigated district, four species were predominant: *A. subpictus*, *A. culicifacies*, *A. annularis* and *A. stephensi*. In particular, the densities of *A. culicifacies* and *A. subpictus* had two high peaks in March and August. Jabalpur had the longest rainy season (July–October) and most abundant annual precipitation (1,500 mm) among all study sites.

The observed mosquito data were collected for both indoor and outdoor resting at the five abovementioned sites with irrigation systems. An adult density at each site was shown in relative value if the density on the peak day was 100 %. The observed period of adult appearance (active growing period) was defined as the time when the relative abundance exceeds more than 25 % (man hour density), because an adult mosquito can appear quickly and malaria can become epidemic under the same conditions (e.g., Rowland et al. 2002; Singh et al. 2004). Likewise, the observed period of adult disappearance was defined as the time when the relative abundance decreased to less than 25 %.

Outline of ECD-mg model

The ECD-mg model (Ohta and Kaga 2012) consists of two processes; the calculation time interval for all processes of the model is 1 day (Fig. 1a). Since the mosquitoes could have grown across different years, the calculation period included more than 2 years to count the generation number of the mosquito. The first process estimates the daily equilibrium of water temperature (T_w) and amount of water in the soil (W) precisely using energy and water balance models (Ohta et al. 1993; Tao et al. 2003; Ohta and Kimura 2007) that are necessary for description of an *Anopheles* habitat during its immature stages. This calculation uses simple climate factors, elevation, soil, and irrigation seasons. The second process calculates the daily progression of mosquito growth based on the life-cycles of an *Anopheles*. If the daily mean $T_{\mathrm{w},k}$ and W_k are suitable for survival on a kth day, the daily growth of the mosquito is accumulated to the growth on the previous ($k-1$) day and the generation number of the mosquito is counted. In this model, the total sum of the generations of all species is counted as a single entity, although there is no consideration for calculations of the generation of each species. Generally, the number of generations per year is one of the most important parameters that affects the abundance of multivoltine species and represents site suitability (Yamamura and Kiritani 1998; Kearney et al. 2009).

This model assumes that the developmental rate of mosquitoes is determined by the temperatures of the habitat under the conditions of sufficient water, because the development of the egg, larval, and pupal stages is dependent on water temperature, and the development of the adult mosquito is determined by air temperature (T_a). Although the developmental rate for each stage with respect to temperature is different for each *Anopheles* species, these data are not available for the four species at each study site. Since the current ECD-mg model cannot handle multiple species with individual parameters, these species are aggregated for modeling purposes. The daily progression of mosquitoes was accumulated using inclusive parameter-values, which were also used in the previous study (Ohta and Kaga 2012).

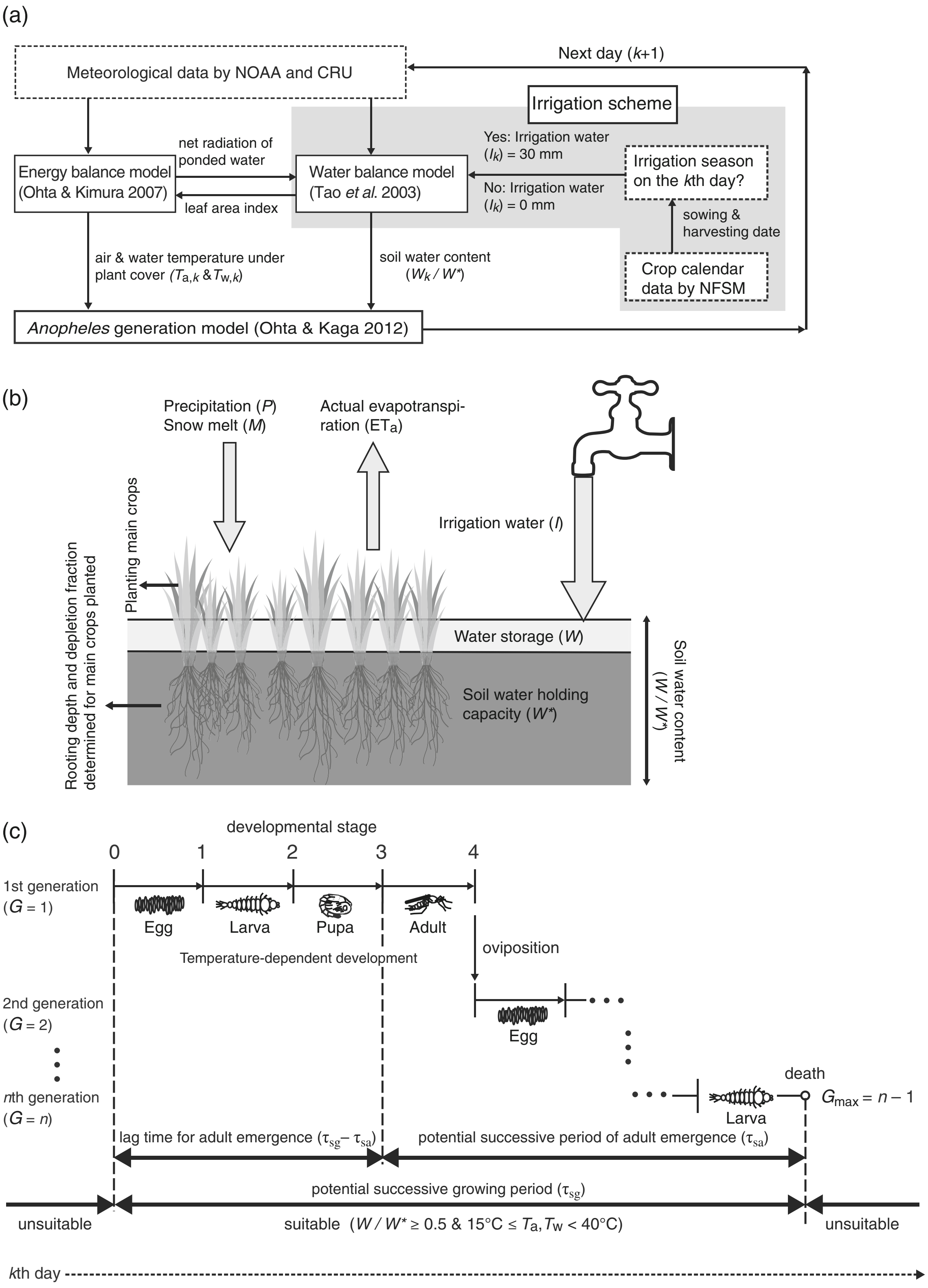
Modified ECD-mg incorporates irrigation scheme into water balance model

In the previous ECD-mg model, the habitats of *Anopheles* were assumed to be areas of natural shallow water with growing grass plants (lowland puddles, which are distributed widely in forests, river basins, and coastal areas), and there was no consideration of man-made sources such as ditches and sewage systems. Therefore, soil-water content was limited mainly by precipitation, the only input factor of water for a habitat. The main modification to the previous ECD-mg model incorporates an irrigation scheme into the water balance equation in the first process (the gray area in Fig. 1a). In the present study, the soil water content at the depth of the plant roots was re-calculated using the water balance approach as illustrated in Fig. 1b. Calculation of the amount of water in the soil on the kth day (W_k, mm) was performed using the following equation:

$$W_k = \min\left(W_{k-1} + P_k + M_k + I_k - \mathrm{ET}_{\mathrm{a},k} \text{ or } W^*\right) \qquad (1)$$

where W_{k-1} is the soil water content at the end of the previous ($k-1$) day, P_k is daily precipitation (mm), M_k is daily snow melt (mm), I_k is daily input irrigation water (mm), $\mathrm{ET}_{\mathrm{a},k}$ is daily actual evapotranspiration on the kth day (mm), and W^* is the water-holding capacity of the soil (mm), which reflects the type of soil texture and organic content as obtained from Dunne and Willmott (1996). When W_k obtained from these calculations was larger than W^*, it was assumed that W_k was equal to W^* (Tao et al. 2003; Ohta and Kaga 2012).

The daily value of M_k was obtained from the calculation methods proposed by Tao et al. (2003). Smith (1992) and Arora (2006) simulated the minimum necessity of irrigation water for cultivation in India, and the daily minimum value of I_k was approximately 10 mm. In addition, a large amount of irrigation water would be required immediately before planting crops. It is strongly dependent on the supply capacity of irrigation water rather than the necessary quantity. In fact, there is a tendency to supply the maximum quantity that can be supplied, and the observational values of daily irrigation water ranged from 10 mm to 45 mm (Hytteborn 2005). In this study, the value of I_k was constant and equal to 30 mm during the irrigation seasons, and this value was assumed to be 0 mm during the other periods (Fig. 1a). The



parameters of the soil's physical properties necessary for estimation of $ET_{a,k}$ are shown in Table 1 (Smith 1992; Allen et al. 1998; Hytteborn 2005). Because crops significantly alter the values of these parameters, the data for the

◀ **Fig. 1a–c** Flow diagram of the modified ecophysiological and climatological distribution of mosquito generations (ECD-mg) model. **a** The *gray* area shows an additional scheme over the previous ECD-mg model (Ohta and Kaga 2012). Prior to the calculation of the growth of mosquitoes, energy balance parameters, such as the net radiation at the habitat, are calculated according to the method used by Ohta and Kimura (2007) with simple climate data. Using the value of the net radiation, the actual evapotranspiration is calculated, and consequently the water balance model is used to estimate whether grass plants can grow. Finally, the water temperature ($T_{w,k}$) and soil moisture content (W_k / W^*) of the habitat is determined by coupling energy–water balance models. **b** Water balance in a typical habitat of *Anopheles* under irrigation. **c** The life cycle of *Anopheles* mosquitoes, and how to count a generation number and growing periods. The daily developmental rate on the *k*th day was determined by the temperatures ($T_{w,k}$ or $T_{a,k}$) of the mosquitos' habitat under sufficient water conditions

main crops during the period from sowing to harvest in India and Pakistan (NFSM 2011; FAS 2012) were used to accurately calculate $ET_{a,k}$ if the observational data on crop seasons were not obtained. In addition, the total available soil water was assumed to be constant at 140 mm (Smith 1992; Hytteborn 2005).

Estimation for potential successive growing period and potential number of generations

The modified ECD-mg model was applied to determine whether the conditions allow for an *Anopheles* mosquito to develop, and the results of the developmental stage reached on a *k*th day can be obtained (Fig. 1c). The maximum developmental stage in the model is defined as the stage that a mosquito can reach on a *k*th day (Ohta and Kaga 2012). A mosquito can become mature (an adult appearance), when the developmental stage exceeds 3. If the developmental growth stage reaches 4, an adult mosquito has the ability to reproduce and oviposit eggs. At the same time, this was counted as one generation of mosquitoes (*G*).

An adult appearance period (τ_a) of mosquitoes can be expressed as the time between the adult stage of the first generation's mosquito and the last generation dying under conditions unsuitable for their development (W / $W^*<0.5$ or $15\ °C>\{T_a, T_w\}\geq 40\ °C$). The first date of adult appearance of the first generation's mosquito and the end date of the last generation were defined as the mosquito appearance date and the mosquito disappearance date, respectively (Ohta and Kaga 2012). The maximum number of generations (G_{max}) was defined as the number of the last existing generation for that year. The values of G_{max} and τ_a were counted over a 1-year period. The value of τ_a corresponds to the sum of the potential successive periods of adult appearance (τ_{sa}), which directly affects the number of the malaria cases.

Table 1 Input parameters of physical properties of soil surface with each crop (after Smith 1992; Allen et al. 1998; Hytteborn 2005)

Main crops	Rooting depth (m)	Soil water depletion fraction (no unit)
Rice	0.7	0.20
Cotton	1.3	0.65
Winter wheat	1.5	0.55
Soybeans	0.9	0.50

The concepts of the potential growing period (τ_g) and the potential successive growing period (τ_{sg}) have been used extensively for estimating the growth and reproduction of mosquito populations by many modeling studies (Martens et al. 1999; Lieshout et al. 2004). The τ_g is defined as the sum of τ_{sa} and the developing period in the immature stages of the first generation. In the present study, the consecutive τ_g period was calculated and was then defined as τ_{sg}. Thus, the difference between τ_{sg} and τ_{sa} is the period from egg to pupa of the first generation (Fig. 1c).

Climate data used with modified ECD-mg model

The water and thermal resources of mosquito habitats were estimated with a 1-day time interval using the modified ECD-mg model and simple climate factors, such as air temperature, precipitation, solar radiation, cloud cover, relative humidity, and wind speed (Fig. 1a). Daily mean air temperatures and precipitation near each study site were adopted from National Oceanic and Atmospheric Administration (NOAA 2011) data. Other climatic data were collected from the Climate Research Unit (CRU), available through the IPCC Data Distribution Center (New et al. 1999). All data were included in the dataset for 1961–1990 climate normals. If daily data were not available for the modified ECD-mg model, monthly values were converted to daily values using linear interpolation to ensure that the daily values were consistent with monthly averages or total values (Ohta and Kimura 2007; Ohta and Kaga 2012).

To verify the versatility of the modified ECD-mg model in this study, we used the abovementioned gridded climate data rather than local observational weather data in published papers; the ECD-mg model is not applicable to other regions without using grid data.

Results

Seasonal changes in mosquito appearance

As shown in the upper panels on Fig. 2, soil moisture content in the irrigated areas was saturated mostly during irrigation periods (solid line) and decreased sharply outside of irrigation periods (dashed line). When the values of W / W^* were calculated for areas without irrigation at the study sites, the condition for more than 50 % soil moisture content suitable for the growth of mosquitoes was limited to 2–3 months, equivalent to the rainy season (July–September).

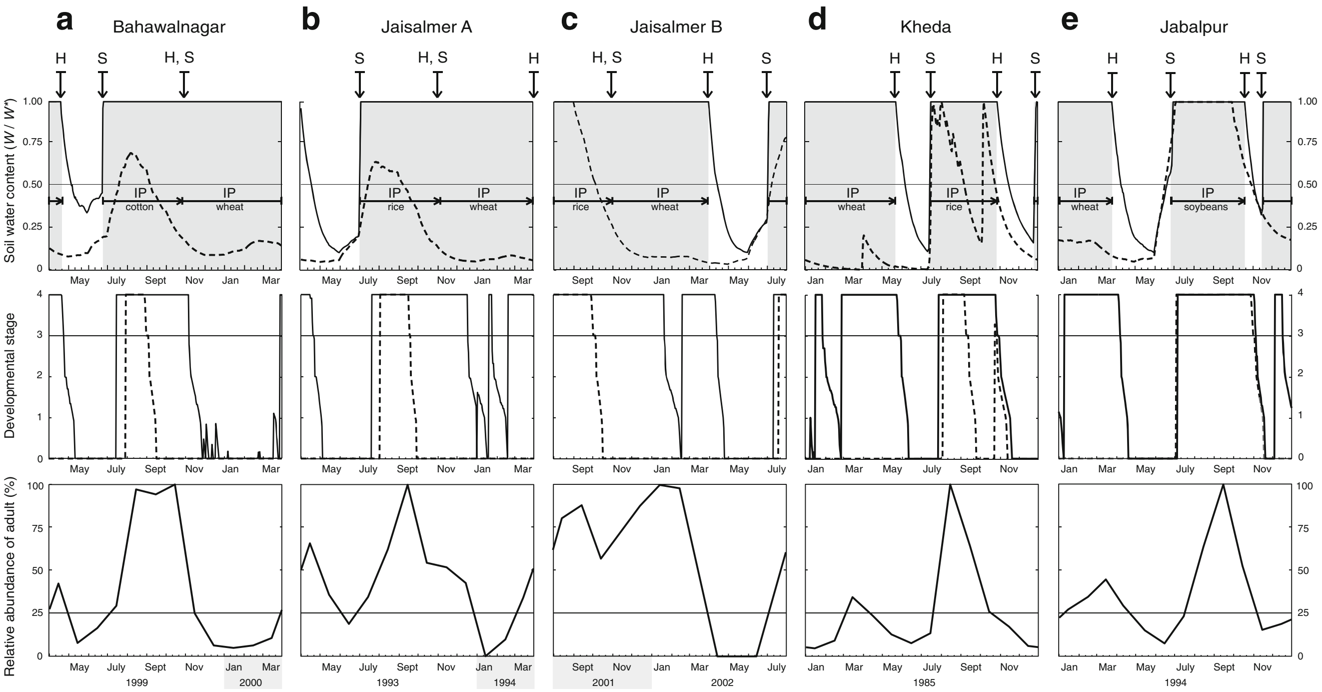


Fig. 2 Temporal variations in the growth of mosquitoes and soil conditions of their habitat. *Upper panels* soil moisture content simulated in this study (*solid line* with irrigation, *dashed line* without irrigation); *middle panels* maximum growth stage of mosquitoes simulated in this study (*solid line* with irrigation, *dashed line* without irrigation); *lower panels* observed data of the relative abundance of adult mosquitoes (Bhatt et al. 1991; Singh and Mishra 2000; Tyagi and Yadav 2001; Herrel et al. 2004; Joshi et al. 2005). *IP* Irrigation periods for main crops, *S* sowing time, *H* harvest time. Each growth stage is expressed in this model; *0–1* egg, *1–2* larva, *2–3* pupa, *3–4* adult

The adult mosquitoes, which exceed maximum growth stage 3, appeared during the period with irrigation except during winter (solid lines in the middle panels of Fig. 2). However, the period of high abundance of adult mosquitoes in Jaisalmer B was also found in winter (lower panels of Fig. 2). When the growth stages were calculated for non-irrigated study sites, adult mosquitoes appeared only in rainy seasons (dashed lines in the middle panels of Fig. 2). The modeled appearance period of adult mosquitoes with irrigation (solid lines in the middle panels of Fig. 2) agreed well with the observed period of high abundance of adult mosquitoes (lower panels of Fig. 2). Also, the high abundance of adult mosquitoes was observed during non-rainy seasons, although the abundance data indicate that mosquitoes were able to survive in low numbers throughout the year (lower panels of Fig. 2).

The dates of the appearance or disappearance of mosquitoes at the observation sites were reproduced by using the previous ECD-mg model that did not incorporate irrigation and the modified ECD-mg model that incorporated the irrigation factor with simple climate data. Results obtained from the modified ECD-mg model with irrigation can explain the observational data of appearance and disappearance dates (Fig. 3a). The root mean square errors (RMSE) between the observed and modeled values for these dates were approximately 10.1 days (appearance date) and 20.1 days (disappearance date). On the other hand, the results obtained from the previous ECD-mg model without irrigation cannot explain the observational data of appearance and disappearance dates (Fig. 3b). The value of the RMSE between the observed and modeled values for these dates was approximately 107.0 days (appearance date) and 129.5 days (disappearance date). The model incorporating irrigation (Fig. 3a) was able to express the observational results well, compared with the model that does not incorporate irrigation (Fig. 3b).

Effects of irrigation systems on appearance period and number of generations

In spring, although there was no appearance of mosquitoes under the simulated conditions without irrigation, τ_{sa} obtained from the modified ECD-mg model with irrigation ranged from approximately 30 to 90 days from the start of irrigation and two to five generations of mosquitoes were attained (Fig. 4a). In rainy seasons, the length of τ_{sa} and the number of G with irrigation (solid lines in Fig. 4b) was doubled compared to those without irrigation (dashed lines in Fig. 4b) at three study sites except for Jabalpur. The most notable result obtained from Fig. 4 is that τ_{sa} and G with irrigation in rainy seasons were higher than those in spring at all sites.

The annual sum of τ_{sa} obtained from the modified ECD-mg model with irrigation ranged from approximately 140 to

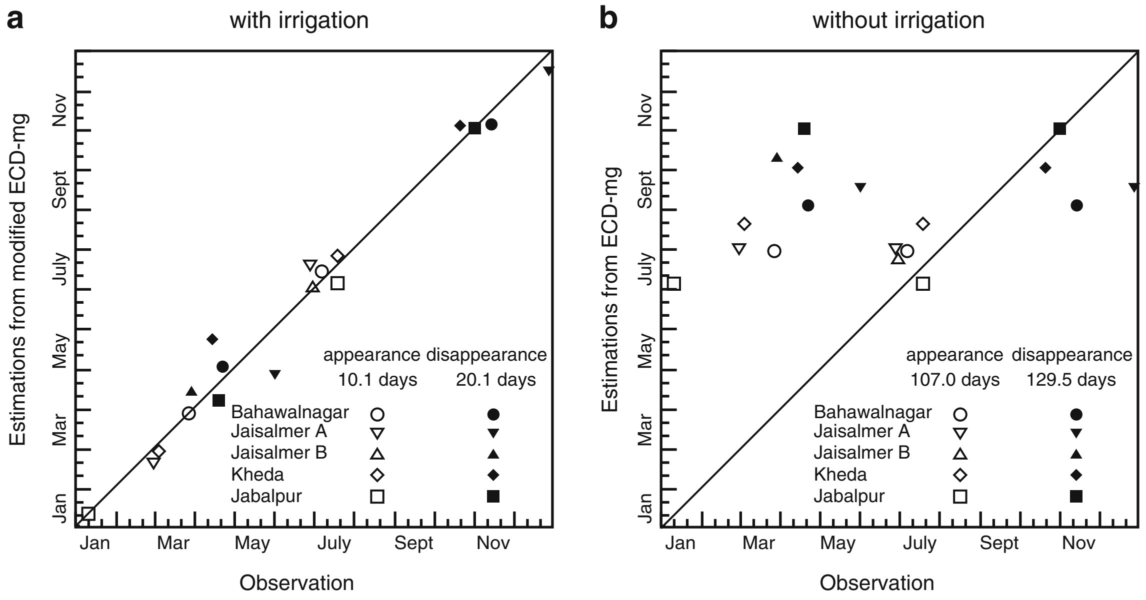


Fig. 3 Comparison of observed and model results for the dates of the start of the appearance and the end of the disappearance for each site under the conditions **a** with irrigation ($P<0.001$) and **b** without irrigation ($P>0.1$). The numbers in these figures show the root mean square errors (RMSE) between the observed and modeled values of these dates. Instantaneous incidence of less than two generations ($G_{\max}<2$) was excluded. The sensitivity analysis, in which the I_k value was changed between 10 mm and 45 mm at 5-mm intervals, shows that the I_k value would likely have had little impact on the accuracy of the model (the appearance date changed from 2.4±1.9 days earlier to 0.7±0.7 days later, in comparison with the reference date when I_k was 30 mm)

290 days (Table 2). In addition, $G_{\max}$ per year calculated using the modified ECD-mg model with irrigation ranged from 10 to 14 generations. On the other hand, the annual sum of τ_{sa} obtained from the previous ECD-mg model without irrigation ranged from 35 to 120 days, corresponding only to rainy seasons. In addition, the values of $G_{\max}$ per year calculated

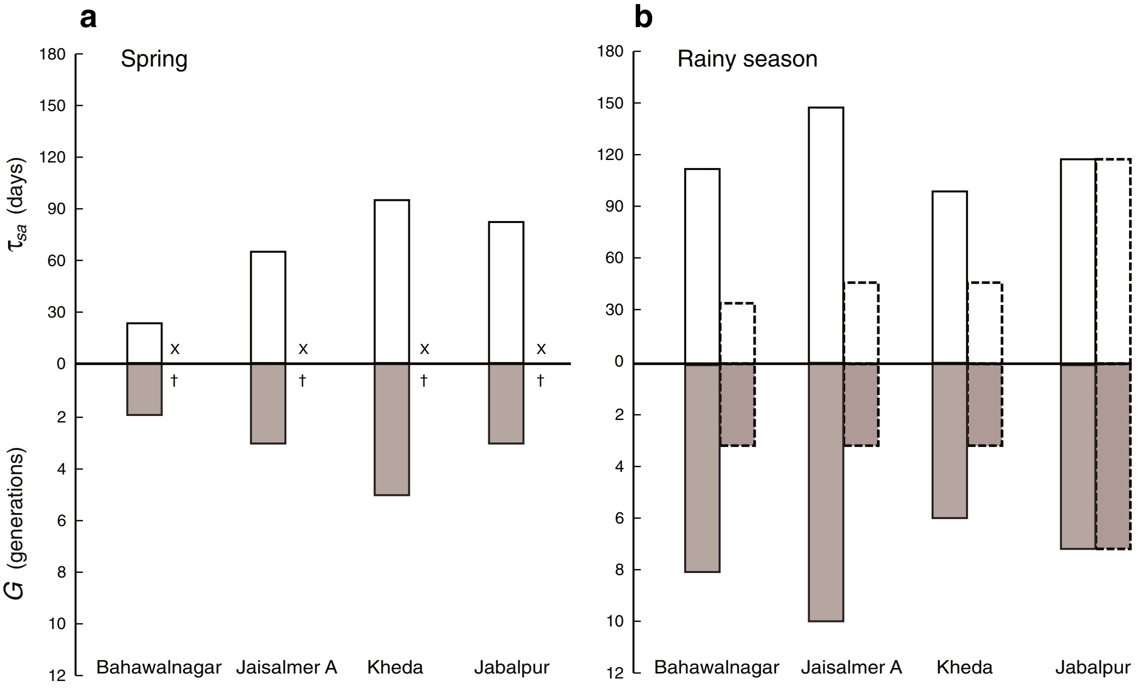


Fig. 4 Differences in the growing periods (τ_{sa}) and the generation number (G) of *Anopheles* mosquitoes during **a** spring and **b** rainy season. *Solid lines* results under irrigation, *dashed lines* results under non-irrigation. Since the growing periods in Jaisalmer B cannot separate spring from the rainy season, it was not regarded as a target for this analysis. *x* No appearance ($\tau_{sa}=0$), *†* no adult appearance ($G=0$)

Table 2 Effects of irrigation on potential successive growing periods and potential number of generations

	Total τ_{sg}	Total τ_{sa}	G_{max}
With irrigation			
Bahawalnagar	170	139	10
Jaisalmer A	248	217	13
Jaisalmer B	295	285	14
Kheda	221	191	11
Jabalpur	239	206	10
Without irrigation			
Bahawalnagar	48	35	3
Jaisalmer A	57	47	3
Jaisalmer B	90	78	5
Kheda	59	43	3
Jabalpur	133	119	7

using the previous ECD-mg model without irrigation ranged from only three to seven generations (Table 2).

Another important result from Table 2 shows that the annual sum of τ_{sa} is shorter by approximately 15–30 days than the annual sum of τ_{sg} under irrigation. In particular, the difference between τ_{sg} and τ_{sa} in Bahawalnagar, Jaisalmer A, Kheda, and Jabalpur is somewhat longer, at approximately 30 days.

Discussion

Irrigation systems lengthen the growing period of the *Anopheles* mosquito

Without irrigation, estimates predicting seasonal changes in the active growing period did not agree with the observed changes in the same period, (dashed lines in the middle panel of Figs. 2 and 3b). Conversely, estimates predicting seasonal changes in the active growing period were able to reproduce correctly observational data when irrigation (item of I in Eq. 1) was included in our modified model (solid lines in the middle panels of Figs. 2 and 3a). Thus, the main factor affecting the active growing period of mosquitoes is an irrigation system, which alters the natural water balance in their habitat. This effect of irrigation on the appearance of the vector species has been also proposed by Konradsen et al. (1998), Kant and Pandey (1999), and Herrel et al. (2001). Our experiment in the present study proved that their hypothesis was plausible.

Under non-irrigation, the active growing period of mosquitoes in west India was assumed to be limited to a few months during the rainy season (dashed lines in the middle panel of Figs. 2 and 4), because the growth period of the *Anopheles* mosquito is limited strongly by the shortage of precipitation in their dry spring. These trends were also found in the results obtained from other research using previous climatic effect models (Martens et al. 1999; Lieshout et al. 2004; Ohta and Kaga 2012).

According to the results found using a modified model that considers irrigation water, mosquitoes were able to grow actively in spring (solid lines in the middle panel of Figs. 2 and 4a) and the growing period in rainy seasons was extended doubly (Fig. 4b) when compared with that under non-irrigation from the changes in the water balance due to water supply from irrigation (solid lines in the upper panel of Fig. 2). On the other hand, our results of seasonal variations in W / W^* during the irrigation period coincide with those by Hytteborn (2005). However, in winter during the irrigation period, adult mosquitoes did not appear at four study sites (solid lines in the middle panel of Fig. 2), because of the paucity of air or water temperatures suitable for survival and growth of mosquitoes. In winter at Jaisalmer B, temperatures that did not drop below 15 °C lead to a consecutive growing period of mosquitoes from rainy season to spring (middle and lower panels of Fig. 2). Although, compared with the rainy season, the number of mosquitoes decreases drastically in a dry summer or winter, the *Anopheles* mosquito lives obscurely in very limited temporary breeding sites, such as riverine sites and dwellings, which have different thermal and/or water conditions from those assumed in the present study (Bhatt et al. 1991; Chandra 2008).

Consequently, the annual growing period was extended significantly by approximately 3–9 months (solid line in the middle panel of Fig. 2, and Table 2) due to irrigation water for agricultural production. These growing periods in west India are equal to the growing periods in the subtropical area across the Indochina Peninsula to southern China (Martens et al. 1999; Lieshout et al. 2004; Ohta and Kaga 2012). Therefore, it can be concluded that west India has a malaria risk equivalent to other humid tropical regions although these areas are categorized as semi-arid regions. These results are not contradictory to the reports that many malaria infections have also occurred in semi-arid regions such as west India as well as in subtropical humid regions (Chareonviriyaphap et al. 2000; Lal et al. 2000; Rowland et al. 2000).

Irrigation systems increase the number of generations of the *Anopheles* mosquito

Since Jabalpur in central India has a longer rainy season, the value of G_{max} under non-irrigation was seven generations (Fig. 4, Table 2). For the other study sites in dryer west India, G_{max} ranged from three to five generations under natural conditions, reflecting the growing period being limited to a few months because of dry conditions during the rest of the year. This low G_{max} value corresponds to the values in cool, temperate zones such as the Korean Peninsula, which is the northern limit of malaria cases (Martens et al. 1999; Ohta and

Kaga 2012). On the other hand, 10–14 generations of $G_{\max}$ under the irrigated conditions have the same numbers of those in tropical humid regions, corresponding to the value of $G_{\max}$ at an epidemic area of malaria such as Myanmar and Thailand (Chareonviriyaphap et al. 2000; WHO 2010; Ohta and Kaga 2011, 2012). Because the present number of malarial cases and the observed appearance of *Anopheles* mosquitoes in west India are examined (Jayaraman 1982; Bhatt et al. 1991; Singh and Mishra 2000; Tyagi and Yadav 2001; Singh et al. 2004; Gupta et al. 2009), the previous model that does not incorporate irrigation underestimates the active growth rate of mosquitoes. Conversely, the realistic growth rate of mosquitoes can be estimated from the modified ECD-mg model that takes into consideration the presence of anthropogenic water due to irrigation (Fig. 3). And even if gridded global climate data were used, it was found that the growth of local mosquito populations could be predicted with sufficient accuracy.

Since it is clear that the population density of mosquitoes increases as the generation number increases, the potential generation number is an important index (Yamamura and Kiritani 1998). Kearney et al. (2009) have used the potential generation number as an index of stabilization of a population of *Aedes* mosquitoes in Australia. The increases in G during the rainy seasons due to irrigation systems in the present study (Fig. 4b) could bring about the increase and stabilization of the population of *Anopheles* mosquitoes. The irrigation system not only enables the active growth of mosquitoes in dry seasons (Fig. 4a), but also plays an important role in bringing about the increase in the potential number of generations in rainy seasons (Fig. 4b).

The possible effects of temperature increases on the generation number of insects have been studied by Yamamura and Kiritani (1998), Kearney et al. (2009), and Ohta and Kaga (2011). According to their research, the increases in $G_{\max}$ per year are 1–2 generations for each degree increase in temperature, which is significantly smaller than the increase in generation number due to irrigation, as shown in Table 2. It is concluded from the above-mentioned discussion that irrigation systems have profound effects on the generation number of mosquitoes. This increase in the number would lead to the alteration of malarial infections through the increase in adult population density (Baeza et al. 2011). Our results suggest that the risk of malaria in semi-arid regions may have increased by the expansion of the irrigation systems.

Adult appearance period is more important than potential successive growing period

The concept of the potential successive growing period (τ_{sg}) has been used in previous studies on the assessment for the risk of malaria disease (Martens et al. 1999; Lieshout et al. 2004). Because the lag time between the start of the development of an egg to adult appearance in the first generation (Fig. 1c) becomes quite small in subtropical humid regions due to the rapid growth of an *Anopheles* mosquito, this lag time has not attracted much attention. However, it is necessary for accurate assessment of malaria risk to estimate correctly the length of the adult appearance period (τ_{sa}). It is especially desirable to exclude the immature period of the first generation that has no relation to transmitting malaria. For this reason, although Craig et al. (1999) and Morse et al. (2005) developed the growth model taking into consideration the growing periods of a larva, their models were not able to eliminate completely immature stages from the life stages of the first generation, because the models have not included the hatching period of an egg and the growing period of a pupa.

On the other hand, the revised ECD-mg model in the present study can specify easily a day when the first generation reaches the adult stage, since our model can predict the immature conditions on a day-to-day basis. The large differences between τ_{sa} and τ_{sg} by approximately 30 days in Bahawalnagar, Jaisalmer A, Kheda, and Jabalpur occurred (Table 2) because there were two immature stages of the first generation in spring and the rainy season (Fig. 2). The period during the immature stage of the first generation that poses a very small risk for malaria infection was much longer than expected (Table 2). The reason for this reduced risk is that parasite development in the mosquito is limited by low temperatures, as well as the presence of only very few adult mosquitoes. Regarding the risk of malarial infection, it is necessary to use the concept of τ_{sa}, which deducts the immature period of the first generation from τ_{sg} (Craig et al. 1999).

Concluding remarks

This study found that anthropogenic changes that increase water in the environment due to extensive irrigation could encourage the growth of *Anopheles* mosquitoes through the alteration of the water balance within their habitat, as also proposed by Konradsen et al. (1998), Kant and Pandey (1999), and Herrel et al. (2001). In other words, it was suggested that the active growth of *Anopheles* mosquitoes is severely restricted if there was no irrigation in semi-arid subtropical regions. The irrigation systems could lengthen the active growing period for *Anopheles* mosquitoes and increase the maximum generation number of mosquitoes in these regions.

Besides irrigation, deforestation and reservoirs have affected the proliferation of mosquitoes through the changes in water balance within their habitat (Ebi et al. 2005; Kearney et al. 2009). It is necessary that these additional factors affecting water balance according to local features at a site should be considered as a next step. When it becomes possible to incorporate anthropogenic factors other than irrigation, the ECD-mg model could predict the growth rate of mosquito populations with more accuracy than the current ECD-mg model.

However, since this model predicts the changes in generations based on the assumption of one individual mosquito, it has a shortcoming that neither seasonal variation nor the number of peak appearance days can be expressed. For example, even if within the time that $G_{\max}$ has not counted, a small number of *Anopheles* mosquitoes may survive obscurely because of the late growth rate. Moreover, in the rainy season, the number of individuals can increase drastically so that generations become shorter and tend to overlap, which cannot be expressed in our model. Also, it is difficult to determine the abundance and dynamics of the *Anopheles* population from the potential number of generations predicted by the current ECD-mg model. Therefore, the structure of this model should be changed to include a population dynamics model that assumes multiple mosquitoes (Morin and Comrie 2010; Gong et al. 2011) from the generation model that describes one individual. Although daily equilibrium temperatures were used to calculate the growth of mosquitoes in the modified model, it will be necessary to change to a higher time-resolution model (Paaijmans et al. 2008), because the possibility exists that the growth rate of an *Anopheles* mosquito is determined by daily maximum and minimum temperatures.

Acknowledgments This study was funded in part by the Ministry of Education, Science and Culture of Japan (Grant-in-Aid for Scientific Research C–21510022, C–24510020) and a Waseda University Grant for Special Research Projects (2010A–088, 2011A–079).

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