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REVIEW

Climate change and malaria transmission

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There is a consensus among climatologists that our planet is experiencing a progressive rise in surface temperature due to the increased production of 'greenhouse' gases. Some of the possible consequences of elevated temperature on malaria transmission are examined in the present review. A simple mathematical model is first used to examine the effect of temperature on the ability of *Anopheles maculipennis* to transmit vivax malaria. This indicates that small increases in temperature at low temperatures may increase the risk of transmission substantially. This is important, since vulnerable communities, poorly protected by health services, in areas of unstable or no malaria are likely to be at increased risk of future outbreaks. In contrast, areas of stable transmission may be little affected by rising temperature. It is thought that global warming will lead to coastal flooding, changes in precipitation and, indirectly, changes in land use. Just how these changes will effect transmission at a regional level requires an understanding of the ecology of local vectors, since environmental changes which favour malaria transmission in one vector species may reduce it in another. Methods for predicting future changes in malaria in different regions are discussed, highlighting the need for further research in this area. Most importantly, there is a need for researchers to validate the accuracy of the models used for predicting malaria and to confirm the assumptions on which the models are based.

The Earth's temperature has risen by 0.3–0.6°C during the last century and there is a consensus amongst climatologists that the rising levels of 'greenhouse' gases are causing the planet to warm (Houghton *et al.*, 1996). The implications of this warming on the world's most important vector-borne disease, malaria, which currently causes about 300–500 million clinical cases each year (WHO, 1993), are the subject of this review. The mechanism thought responsible for climatic change is described and some of the major limitations of

the mathematical models used to make climate forecasts are discussed. Subsequently, the effect of temperature on transmission is illustrated by considering the case of vivax malaria transmitted by a European vector of malaria. This is followed by a discussion of how climate change is likely to affect different vector systems at a regional level. Finally, the methods used for forecasting malaria in a changing world are critically reviewed.

GLOBAL WARMING

Our planet is enveloped by gases that allow solar radiation to pass through the atmosphere.

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Much of the long-wave radiation which is emitted from the Earth's surface is absorbed in the atmosphere and partly re-emitted to warm the surface of the globe. At present, the average surface temperature of our planet is about 15°C but, without the insulating layers of 'greenhouse' gases, the temperature would drop by 33°C (Houghton *et al.*, 1990). Of these greenhouse gases, CO₂, produced by animals and plants and by burning fossil fuels, is the most important. Trees are major consumers of this gas and hence deforestation contributes to an increase in CO₂ in the atmosphere. There are also other greenhouse gases, occurring at lower concentrations than CO₂, which are, collectively, just as important. These include chlorofluorocarbons (CFC), CH₄, N₂O, O₃, CO and water vapour. CFC are synthetic molecules produced, as gases, for cooling refrigerators and bubbling foam and as aerosol propellants. Methane results from the breakdown of plants in bogs, swamps and rice fields and during digestion in ruminants. The major sources of N₂O are uncertain, but may be related to agricultural practices such as the burning of organic material and the application of fertilizer. Ozone is produced by the breakdown of hydrocarbons, nitrous oxides and CO by sunlight. The level of water vapour may increase further with global warming, as increased heating of the oceans and inland bodies of water occurs.

Predicting Changes in Climate

Measurements from air bubbles trapped in ice cores extracted from the Antarctic demonstrate that the levels of CO₂ have fluctuated widely over the past 160 000 years (Barnola *et al.*, 1987). Most importantly, there is a close association between CO₂ levels and temperature (Jouzel *et al.*, 1987), although it is not known whether the CO₂ levels drive the climatic changes or *vice versa*. Levels of CO₂ are presently unprecedented and have risen inexorably by about 30% since pre-industrial times (Houghton *et al.*, 1996). Recordings from Hawaii have shown that the recent output of CO₂ has accelerated, having risen from about 310 ppm in 1958 to over 350 ppm in the late 1980s (Keeling *et al.*, 1989).

In order to predict future climatic changes, complex mathematical models, which take into account the major factors governing the Earth's climate as well as estimate the future production of greenhouse gases, have to be developed. The type and scale of future changes are matters of some controversy. Predictions are based on computations made from a number of different general circulation models (GCM). Each of these consist of a series of mathematical expressions which attempts to summarize the complex interactions between the surface of the Earth and the atmosphere. The six scenarios postulated by the Intergovernmental Panel on Climatic Change (IPCC) are intended to cover the range of most likely possibilities for the future production of greenhouse gases (Houghton *et al.*, 1990). Assuming that human activity does not alter substantially in the future and that atmospheric concentrations of CO₂ double relative to present levels, the models forecast increases of about 2°C by 2100 (Houghton *et al.*, 1996). This increase is equivalent to the difference between global temperatures experienced during the last ice age and today.

Although GCM are able to simulate today's climate at a global level, their accuracy and ability to describe future changes will remain in doubt for at least another decade (Houghton *et al.*, 1990, 1992). The ability of GCM to forecast extremes of climate is limited compared with their ability to measure mean changes in climate (Houghton *et al.*, 1990, 1992). This uncertainty may simply reflect our poor understanding of how climate and the hydrological cycle interact (Anon., 1992; Chahine, 1992) or it may be that the climatic system is too complex for man ever to predict small-scale events with much accuracy. There are simply too many uncertainties about the future to make any forecast reliable. For example, only calculated guesses can be made as to the scale and pattern of changes in our planet's population, living conditions, industry and land use; particularly as economic development and the distribution of wealth within societies is so heterogenous. Neither major technological breakthroughs which could reduce the emissions of greenhouse gases nor

the responses of individuals and governments to environmental, economic and political pressures can be foreseen.

TEMPERATURE AND VECTORIAL CAPACITY

Clearly, there is a great deal of uncertainty surrounding man's ability to predict the type, distribution and scale of climatic change accurately. However, could changes in the environment be more accurately linked with factors affecting the transmission of malaria? How will future temperature effect the vectors and the malaria parasites they transmit?

Insects must be well adapted to the environment in which they are found. They are able to withstand the effects of normal climatic variations and can seek out microclimates that offer protection against extremes of climate. They can adapt their behaviour to the most favourable part of the diurnal cycle. Where extremes are predictable and of long duration, they can aestivate. Aestivation occurs among some temperate mosquito species during cold winters (Swellengrebel, 1929) and among some tropical mosquitoes during hot, dry seasons (Omer and Cloudsley-Thompson, 1970). Catastrophic climatic events which exceed this capacity cause large-scale mortality of the population and temporarily interrupt transmission. This review is concerned with relatively stable climatic conditions which endure for at least the period required for the development of parasites within the mosquito (10–30 days). Since both the vectors and the parasites they transmit are poikilotherms, elevated environmental temperatures generally enhance the rate of development and activity of these organisms, thus helping to increase the transmission of parasites. This risk of transmission can be expressed mathematically as vectorial capacity (i.e. the potential number of inoculations which originate from one infective person each day).

In order to examine how a rise in temperature could effect the transmission of vector-borne diseases, the relationship between temperature and the vectorial capacity of

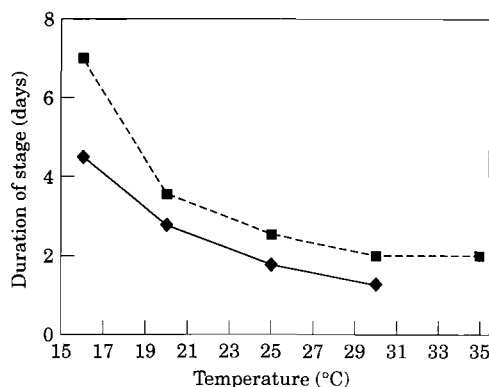


Fig. 1. Development of eggs (■) and pupae (◆) of *An. minimus* at different temperatures (Muirhead-Thomson, 1951).

Anopheles maculipennis, a European vector of malaria, in the transmission of *Plasmodium vivax* was explored. One common form of the equation for vectorial capacity (C) is shown below:

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

where ma is the person-biting rate, a the person-biting habit, n the period of parasite development in the vector (extrinsic period of development) and p the probability of a vector surviving 1 day. Perhaps not surprisingly, most of the parameters which are used in the vectorial capacity equation are influenced by temperature.

The person-biting rate is a measure of the number of times an adult gets bitten each day. Biting rates are dependent both on the number of mosquitoes/person and the feeding behaviour of the vectors. The numbers of adult mosquitoes in an area can be partially dependent on the rate at which these insects are produced from their breeding sites. The relationship between temperature and the rate of development of two of the aquatic stages of *An. minimus* is shown in Fig. 1. Although small increases in temperature at low temperatures have a greater effect on development time than similar changes at higher temperatures, the rate at which populations of mosquitoes

TABLE 1
Threshold temperatures and duration of gonotrophic cycle for three malaria vectors

Parameter	Anopheles species		
	maculipennis*	culicifacies†	stephensi†
f_1 (degree days)	36.5	29.7	43.4
Threshold temperature, g_1 (°C)	9.9	12.6	8.9

*Data from Detinova (1962).

†Data from Mahmood and Reisen (1981).

increase is generally more rapid in warm climates than in colder ones. However, as the main factor limiting the numbers of mosquitoes in any area is generally the availability of mosquito breeding sites, high numbers of mosquitoes can be found in temperate areas as well as tropical ones. In northern Canada, for example, an exposed forearm was bitten almost 300 times in 1 min (Gillett, 1974). The cost of rapid development at higher temperatures is that smaller and less fecund adults are produced than at more favourable temperatures (Clements, 1992). At extremely high temperatures, $>30^\circ\text{C}$, development actually slows down, as has been shown for *Toxorhynchites brevipalpis* (Trpis, 1972).

The person-biting habit is the mean frequency at which mosquitoes feed on people. In the wild, tropical mosquitoes usually bite at regular intervals of 2–5 days. Small changes in temperature can again make a large difference. For instance, although *An. gambiae* and *An. funestus* will feed every 2 days at around 25°C , they only feed every 3 days at lower temperatures (Gillies, 1953). For a population of mosquitoes, the shortening of the interval between bloodmeals with increasing temperature can be described by a smooth curve, the minimum gonotrophic interval being 2 days. The general relationship between a development cycle and temperature is:

$$n, u = \frac{f}{T - g} \quad (2)$$

where f is a thermal sum, measured in degree-days, representing the accumulation of tem-

perature units over time to complete the development, g a development threshold below which development ceases and T is ambient temperature. This relationship applies to the gonotrophic cycle, u (Table 1). As an example, this relationship is shown in Fig. 2 for *An. maculipennis*, with a threshold temperature of 9.9°C and 36.5 degree-days above this threshold (Table 1; Detinova, 1962; Mahmood and Reisen, 1981).

In the U.K., near Liverpool, the woodland mosquito *Aedes cantans* has a gonotrophic cycle in June of about 11–15 days and a survival rate/gonotrophic cycle in the range 0.4–0.5

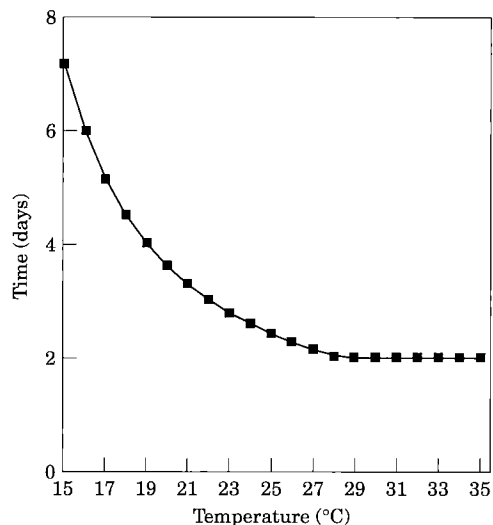


Fig. 2. Duration of gonotrophic cycle (interval between bloodmeals) of *An. maculipennis*.

TABLE 2
Threshold temperatures and duration of sporogony for three species of malaria parasite
in *An. maculipennis* (Detinova, 1962)

Parameter	Plasmodium species		
	vivax	falciparum	malariae
f_2 (degree days)	105	111	144
Threshold temperature, g_2 (°C)	14.5	16	16

(Renshaw *et al.*, 1994). In most situations in tropical climates, although the survival rate of exophilic mosquitoes/gonotrophic cycle is similar, at about 0.4–0.6 (Gillies, 1963; Birley, 1990; Hii *et al.*, 1990), the duration of the gonotrophic cycle is considerably shorter, at just 2–5 days. The survival rate of exophilic species per cycle therefore seems to be relatively independent of temperature. This is to be expected on theoretical grounds (Birley, 1984; Saul *et al.*, 1990), providing the mosquito population is stable and well mixed. The survival of a mosquito should depend on its behaviour and the risk of mortality should be highest when it is seeking a bloodmeal or ovipositing and lowest when it is resting to digest a bloodmeal. In the idealized cycle, feeding and egg laying occur once per cycle and this is independent of the duration of the cycle. The blood-digestion phase, on the other hand, is temperature dependent. Endophilic vectors, resting in more sheltered environments, may, in certain situations, have slightly higher survival rates than exophilic species (Gillies and Wilkes, 1963, 1965; Garrett-Jones and Shidrawi, 1969). Extremes of temperatures will increase mortality. There is a threshold temperature above which death ensues and a lower one, below which mosquitoes become torpid and eventually die.

The length of time required for the development of the malaria parasite within a mosquito (n) is also linked to ambient temperature in a way similar to that shown in eqn 2. For each species of parasite, there are two critical parameters, f and g , just as for the gonotrophic cycle. These values are shown for three species of malaria parasites in Table 2. Macdonald's

graph (Macdonald, 1957) illustrating the relationship between temperature and n for *P. vivax* is shown in Fig. 3. Although this particular graph is regularly redrawn in the literature, it should be appreciated that there is a large scatter between points because the data were based on many different sources. The smooth line is based on eqn 2, using only the *maculipennis* data. Critically, small increases in temperature at low temperatures lead to large reductions in development time.

There is also a little uncertainty about what the minimum temperature is for parasite development; values range from 14.5–16°C for

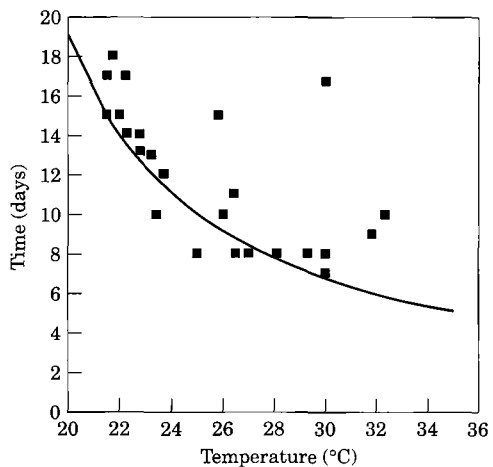


Fig. 3. Duration of sporogonic cycle (period required for parasites to become infective in the vector) of vivax malaria in *An. maculipennis* at different ambient temperatures, estimated using Detinova's equation (Detinova, 1962) and excluding a point of 38 days at 16°C.

P. vivax and 16–19°C for *P. falciparum*. Extremely high temperatures, around 35°C and higher, are lethal to developing parasites (Garnham, 1964).

For any given value of temperature between 15 and 35°C, a value for each parameter in the vectorial capacity equation for *An. maculipennis* has now been estimated. These calculations were based on the following information:

Numbers of Vectors/person, m

It was assumed that mosquito numbers did not rise with temperature and that m equalled 716, so that ma equalled 10 bites/person-night at 15°C.

Human-Biting Habit, a

$$a = \frac{h}{u} \quad (3)$$

where h is the proportion of blood-fed *An. maculipennis* which has fed on people and u is the length of gonotrophic cycle. In nature, h varies from 0.0–0.7 but is usually low (Horsfall, 1955). For the present exercise, h was assumed to equal 0.1.

Daily Survival, p

$$p = 0.5^{(1/u)} \quad (4)$$

For the analysis, 50% of the mosquitoes were assumed to survive each gonotrophic cycle at temperatures between 15 and 35°C.

Gonotrophic and Sporogonic Cycles

The temperature relationship of both gonotrophic and sporogonic cycles was assumed to be as indicated in eqn 2, using the parameters for vivax malaria and the *maculipennis* data. However, it is possible that there may be variation between species and strains of vectors and of parasites.

Vectorial Capacity

The distribution produced from the analysis (Fig. 4) has one important feature. That is, in cold climates, small increases in temperature can result in disproportionately large increases in the intensity of transmission. The form of

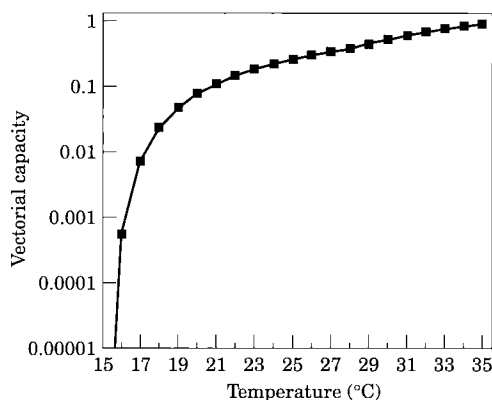


Fig. 4. Effect of rising temperature on the vectorial capacity of *An. maculipennis* for vivax malaria.

the distribution curve is heavily dependent on changes in u and n with temperature. The kink in the curve at 28°C is due to the minimum value of u becoming fixed at its lowest value of 2 days.

Figure 4 represents a sketch of how the vectorial capacity of one temperate vector of malaria may change with increasing temperature. However, it is clear that the relationships between climate and transmission potential are only partially understood and then only for a small number of important vectors. There is a real need to test these relationships in the field in order to improve our understanding of the relationship between temperature and transmission. Moreover, there are several important limitations to the present approach. Vectorial capacity is not a precise tool for measuring the risk of transmission. It is difficult to put statistical confidence limits on vectorial capacity, but these are likely to be wide. Moreover, a number of assumptions used for deriving the equation are false (Dye, 1986). For example, it is assumed, wrongly, that mosquito survival is independent of age and that the mosquitoes feed on their hosts at random. Because of these and other limitations, estimates of vectorial capacity are best used for making broad comparisons.

The present analysis highlights some important areas where further studies are required. Firstly, more information is needed

about the feeding behaviour of vectors. There is an optimal range of temperatures at which mosquitoes feed: around 30°C for tropical mosquitoes and lower for temperate species. This feeding zone is described best by a normal distribution in which extreme values of temperature result in feeding inhibition, as shown for *Ae. aegypti* (Christophers, 1960). The shape of this curve may be of fundamental importance to the way vectorial capacity is affected at extreme temperatures where biting or, perhaps more critically, flight activity declines and stops. Secondly, it is not known with any great confidence at what point high temperatures become lethal to developing parasites. Thirdly, it is unclear whether, at high temperatures, most mosquitoes find cool places to rest. Fourthly, the present analysis is only concerned with mean temperatures and it would be interesting to know how fluctuating temperatures, as occur in Nature, effect some of the biological processes involved in malaria transmission. Lastly, the impact of temperature is considered here in isolation but there are several other environmental parameters which change with increasing temperature, chief of which is relative humidity. Whilst global warming is thought to have little effect on overall relative humidity (Mitchell and Ingram, 1992), periods of excess rainfall or drought, associated with climatic change, would result in large swings in relative humidity in affected areas. The humidity measured at meteorological stations, outdoors in a Stevenson screen, may also differ greatly from that experienced in the micro-environments where vectors actually shelter. For example, vectors which rest indoors are often protected from a low outdoor humidity, and the range of humidity experienced indoors can be much less than that recorded in a screen (Haddow, 1942). The relationship between mosquito survival and humidity is far from clear. There are several reports based on laboratory experiments. However, survival in laboratory cages, in which conditions are uniform, is unlikely to mimic that in the field, where the vectors have opportunities to seek particular microclimates (although these may be density limited). In India, Pal (1943) found a significant variation

of survival of *An. culifacies* with temperature and humidity; at low temperatures survival was highest in saturated conditions whereas humidity was less important at higher temperatures. Mehta (1934) presented results which, on re-analysis, prove to be not significant statistically and this could be a general problem with earlier observations. Thomson *et al.* (1996) suggested that longevity may be a function of saturation deficit. There is a clear need for a review of the subject, supported by further laboratory studies using different mosquito species. Gill (1928) believed that prolonged periods of elevated humidity, which increased the survival of vectors, were the main driving force behind malaria epidemics in the Punjab. A similar explanation was also proposed for epidemics in Venezuela (Alvarado, 1942; Caicedo, 1946). Humidities near saturation have been shown to be unfavourable to a number of tropical vectors of malaria, such as *An. culicifacies*, *An. minimus* and *An. subpictus* (Mehta, 1934; Leeson, 1939). This relationship may not, however, hold for vectors in temperate lands (Muirhead-Thomson, 1951) and the vectors in humid tropical rainforests seem well adapted to high humidities (Charlwood *et al.*, 1985).

Whilst it would be inappropriate, on the basis of the current analysis, to state how much the risk of transmission would increase with rising temperature, the shape of the curve in Fig. 1 may be more revealing. It appears that, as Gillett (1981), Haines and Fuchs (1991), Bradley (1993) and Martens *et al.* (1994) have already suggested, small increases in temperature in cold climates could appreciably enhance the risk of malaria transmission, allowing the vectorial capacity to rise above a threshold where malaria transmission could be maintained.

REGIONAL CHANGES IN CLIMATE

Broad generalizations, about how a small rise in temperature may influence transmission, were made above. In order to make predictions for specific regions of the world, one needs to understand the local geography of the area, the

habits of local vectors and the human factors affecting transmission. It is also important to appreciate that different malaria vectors have adapted to living in specific types of habitat, so that one type of environmental change may increase exposure to malaria in one area and decrease it in another.

Direct Effects of Temperature

In many parts of Africa malaria is endemic and may be acquired throughout the year. The principal vectors in these areas, *An. gambiae* s.s., *An. arabiensis* and *An. funestus*, have a vectorial capacity frequently greatly in excess of that needed to maintain the cycle of infection in local communities. Exposure in some areas can be so intense that almost all children become infected before they are 1 year old. However, many of those that survive this parasitological onslaught will go on to develop a degree of protective immunity against re-infection. In these instances, any increase in vectorial capacity due to elevated temperatures would not be expected to affect greatly the clinical pattern of malaria found in local communities. More dramatic effects would be anticipated in areas of fringe transmission where people are poor and may have little or no immunity against malaria parasites. In Africa, the limits of transmission are often defined by altitude, as altitude and temperature are inversely related. Global warming could push malaria transmission up the slopes to higher altitudes, resulting in epidemics amongst previously unexposed individuals. There are already reports of increasing numbers of cases of malaria in the highlands of Ethiopia and Madagascar (WHO, 1992). In Rwanda, Loevinsohn (1994) recently found that increases in temperature and rainfall were associated with a steep rise in the incidence of malaria and, as anticipated, the increase in the numbers of clinical episodes of malaria was greatest in people living at relatively high altitudes.

Small rises in global temperature may also allow vectors to extend their range laterally without changing altitude. Particular areas of concern are some of the former republics of the Soviet Union which have proved to be

suitable for the growth of anopheline populations and the spread of malaria in the past. Between 1934 and 1936, for example more than nine million cases of falciparum and vivax malaria were reported annually in the Caucasus and the Volga river basin (Bruce-Chwatt, 1988). With the political and social instability in this and other parts of central Asia, and the subsequent deterioration in local health services, the resurgence of malaria seems increasingly likely.

Global warming may also extend the season of malaria transmission in some areas. This can be important, as illustrated by a recent study in the North West Frontier Province in Pakistan (Bouma *et al.*, 1994a), in which unusually high temperatures at the end of the normal malaria season were found to prolong transmission and substantially increase the number of cases of falciparum malaria. In the future, GCM may help to improve prediction of epidemics, by identifying epidemic-prone areas (i.e. those regions which experience marked changes in climate from year to year).

Mosquitos are likely to be amongst the first organisms to extend their range as new areas become environmentally favourable, because of the rapidity with which many mosquito species can increase their numbers. This is particularly true for pioneer species such as *An. gambiae*, which can quickly colonize recently flooded areas. However, the introduction of vectors into new habitats often occurs in an unpredictable manner. The classical example of the dangers posed by new vector species is that of the accidental introduction of *An. gambiae* into Brazil from West Africa in the 1930s (Soper and Wilson, 1943). Transmission by this vector led to a malaria epidemic in 1938, with 100 000 cases and 14 000 deaths. Fortunately, a highly effective vector-control programme was initiated and this resulted in the eradication of *An. gambiae* from Brazil. There have been other epidemics which have been blamed on the introduction of the same vector, including one in Mauritius before 1865, which resulted in the death of a quarter of the inhabitants of Port Louis, and a similarly devastating epidemic in Durban around 1906 (Macdonald, 1957).

On a cautionary note, although it may be tempting to blame recent and future outbreaks on long-term changes in climate, outbreaks may arise due to other, more direct, human activities, such as those caused by changes in land use, the movement of non-immune refugees into malarious belts as the result of war or famine, and the failure of control activities. Moreover, an apparent increase in malaria incidence may simply arise from improved surveillance.

Coastal Flooding

Global warming may lead to an expansion of the surface layers of the oceans and melt the polar ice-caps. In consequence, sea levels are expected to rise by about 50 cm by 2100, resulting in coastal flooding in many areas (Houghton *et al.*, 1996). This could lead to an increase in those vectors that breed in brackish water, such as the malaria vector *An. sudaicus* in South-east Asia. Conversely, saltwater contamination of inland water could help reduce disease transmission. For example, in Africa, freshwater members of the *An. gambiae* complex are generally more efficient vectors than *An. melas* and *An. merus*, their saltwater-tolerant relatives (Coluzzi *et al.*, 1979) [although sporozoite rates in *An. melas* in Guinea Bissau were comparable with those in *An. gambiae* s.s. (Jaenson *et al.*, 1994)]. Thus, replacement of freshwater breeders with saltwater ones could lead to reduced transmission.

Rainfall

Climatic change will probably have an uneven impact on water resources in different parts of the world, although the magnitude of the effects is uncertain. Some areas will have more rainfall than present and others less (Tegart *et al.*, 1990).

In the drier regions of Africa, such as the Sahelian belt, relatively small differences in rainfall and soil moisture content can lead to substantial changes in the ecology of the area and consequent differences in the composition of the populations of the mosquito vectors. For example, certain chromosomal variants of *An. gambiae* are commonly associated with arid conditions, the frequency of the

2La inversion increasing along a transect from the moist forests of the south to the dry savanna in the north (Coluzzi *et al.*, 1979). Although this inversion is therefore likely to increase in importance if desertification in this region continues, it is uncertain how the environmental changes will affect disease transmission. If there is less rainfall, the desiccation of mosquito breeding sites would, in most instances, lead to a reduction in the exposure of local communities to infective mosquitoes. If drought conditions persist, however, people may be forced to migrate to wetter areas where there are more vectors. Thus, highly vulnerable populations of non-immune and poverty-stricken individuals may concentrate in a malaria-endemic area without adequate health care, in ideal conditions for the eruption of an epidemic. Prolonged periods of drought can also result in rivers drying out, producing small pools of water along the old river bed. In Sri Lanka, such conditions provide ideal breeding sites for *An. culicifacies* and have resulted in major epidemics of malaria in the past (Wijesundera, 1988).

If rainfall increases it is most likely to lead to a proliferation of breeding sites and thus enhance the transmission of parasites. In the past, many regional epidemics of malaria in the Far East have occurred following heavy rains in areas where rivers have overflowed and created conditions suitable for a rise in transmission (Gill, 1928). However, excessive rainfall may also reduce the intensity of transmission in certain situations. Mosquito species which breed in slow-moving streams or in pools on dried-up river beds may be flushed out by increased stream flow. During the breeding of *An. farauti* in Papua New Guinea, for example, heavy rain can breach sandbars, flush out immature stages and consequently reduce the number of subsequent adult mosquitoes (Charlwood *et al.*, 1985).

The El Niño-Southern Oscillation (ENSO) is a natural meteorological phenomenon which occurs every 2–10 years and tends to exaggerate the extremes of climate in specific regions of the world (Ropelewski and Halpert, 1987). Thus some areas will experience frequent periods of drought whilst other areas will be

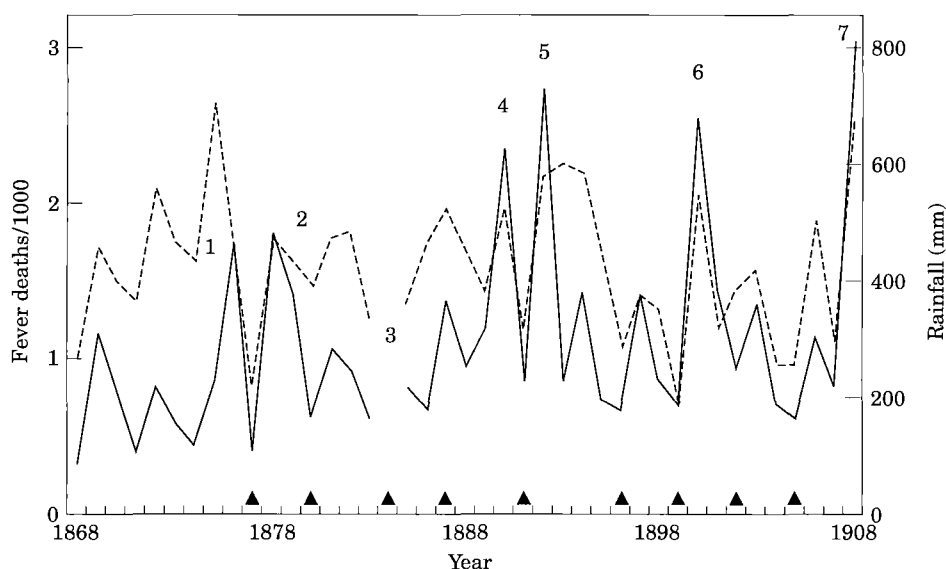


Fig. 5. Relationship between fever deaths (—), most probably due to falciparum malaria, and rainfall (---) in the Punjab (Christophers, 1911). (▲), El Niño-Southern Oscillation years (Ropelewski and Halpert, 1987). Major epidemics are numbered 1–7.

susceptible to years with excessive rainfall. Bouma *et al.* (1994a, b) found that many areas which experienced periodic epidemics were found in ENSO-affected areas and suggested that ENSO events are the driving force behind these outbreaks. To an extent this may well be true, since heavy rains associated with El Niño have resulted in recent outbreaks of malaria in Bolivia, Ecuador and Peru (Nicholls, 1993). In the Punjab, where ENSO years are relatively dry, there was an increase in malaria deaths in 7 or 8 of the 9 years following an ENSO year between 1868 and 1908 (Fig. 5). However, only three of the seven epidemics came in years following an ENSO event and thus ENSO may not be such a good predictor of major epidemics. To what extent global warming will affect these ENSO-related precipitation patterns is not known.

Deforestation

Areas which begin to dry up will tend to lose their tree cover and the loss of forest can have serious effects on the local ecology of malaria. In Africa, for example, malaria transmission

may increase in deforested areas since the most efficient vectors in the *An. gambiae* complex prefer to breed in freshwater in open, sunlit pools. Disappearance of the forest can also lead to a rise in temperature of 3–4°C (Hamilton, 1989), thereby contributing to an even greater potential for the spread of malaria. Indeed, it has been suggested that the reduction in forest cover in the Usambara mountains in north-eastern Tanzania has been partly responsible for the introduction and increasing prevalence of malaria at the top of the hills (Matola *et al.*, 1987). Similarly, destruction of tropical rain-forest in Amazonia has led to an increase in *An. darlingi* in many areas (Walsh *et al.*, 1993) and this, coupled with the influx of migrant workers into the forests (Marques, 1987; Coimbra, 1988; Prothero, 1991), some of whom were infected with malaria parasites, has led to a 76% increase in malaria in this region over a 15-year period (Sawyer, 1986). In contrast, deforestation in Thailand has reduced the breeding sites available for the major vector *An. dirus*, which occurs in dense forest (Walsh *et al.*, 1993).

Irrigation

In regions where rainfall declines, the need for irrigation for crop production will become more urgent. Often irrigation schemes provide vectors with potential breeding sites. The development of rice fields in some parts of West Africa, for example, has increased the transmission of malaria relative to that in adjacent areas (Coosemans *et al.*, 1985). However, in contrast, there are communities living next to areas of irrigated rice which have less malaria than adjacent areas without irrigation (Couprié *et al.*, 1985; Lindsay *et al.*, 1991), perhaps as a result of a general improvement in living standards in irrigated areas, the increased use of bednets and antimalarials and/or density-dependent effects. Large-scale, water-development projects, such as the construction of the Sind irrigation scheme in India (Covell and Baily, 1936), have also resulted in increased malaria.

FORECASTING DISEASE CHANGES

Basically there are two types of approach to forecasting disease: experimental and empirical. In the experimental approach, scientists examine the relationships between a single climatic variable and different parts of the life-cycle of the parasite and vector. These different compartments are then combined in a series of mathematical expressions in an attempt to summarize the relationship between the environment and disease. Such an approach was adopted by Sutherst and Maywald (1985) and Sutherst (1993), who used a computerized system called CLIMEX to examine the suitability of different habitats around the globe for a range of vector species and to assess the risk from malaria in different places (Sutherst, 1993). The assessment was based on an 'ecoclimatic index' that attempts to describe the capacity of insect populations to increase during favourable periods and persist when the climate deteriorates each year. This index is governed largely by the temperature and moisture requirements of the vector; other major factors known to regulate transmission, such as the habits of local vectors, the availability of suitable breeding sites, the

microclimate experienced by vectors and local land-use patterns, are not taken into account. It remains to be tested how this suitability index relates in practice to the abundance of malaria vectors and vectorial capacity.

Martin and Lefebvre (1995), in a similar approach to that of Sutherst and his colleague, developed a Malaria-Potential-Occurrence-Zone (MOZ) model that was designed to predict the intensity and extent of malaria based on the five most popular GCM. This model attempts to predict the potential risk of transmission on the bases of the minimum and maximum temperatures required for parasite development and an estimate of moisture. The MOZ model corresponded fairly well with the distribution of malaria in the 19th century (Wernsdorfer and McGregor, 1988) and in the 1990s (WHO, 1993), after allowing for areas where malaria had been successfully eradicated. Perhaps the most important conclusion from this study was that all five GCM predicted an increase in seasonal malaria, at the expense of perennial transmission. The implication of this is a move towards unstable malaria and an increase in epidemic malaria. Whilst the MOZ model appears to be accurate on a global scale, its accuracy on a regional scale, like that of most models, is not known. There is a clear need to validate all models on a regional scale, using historical or contemporary data sets.

Modelling malaria and climate can become highly complex, as illustrated by a model recently developed by Martens *et al.* (1994, 1995a, b), who examined how climate change might effect malaria across the globe. This model differs from others in that it takes a broad approach to investigating the impact of climate change on malaria, using a function referred to as the 'epidemic potential'. This is proportional to the expected infective life and thus, conceptually, no different to the vectorial capacity at constant density. It includes inputs describing climate, vectors, parasites, hosts and health impact and indicated that an additional 50–80 million cases may occur each year as a direct result of a rise in temperature of 3°C by 2100. Whilst this model is to be applauded for its scope, there are, inevitably, some weak-

nesses with this approach. For example, it is difficult to foresee how land-use changes, improvements in health services or socio-economic development would affect transmission. Moreover, the expected infective life of an average mosquito, E , is based on the daily survival rate rather than the survival during one gonotrophic cycle. The 'universal relationship between temperature and daily survival probability' is a plateau which drops sharply at 35°C (Martens *et al.*, 1994). In the present analysis (see above), the survival rate per gonotrophic cycle was assumed to be constant over a wide temperature range, although the existence of upper and lower lethal temperatures was acknowledged; daily survival rate was thus dependent on changes in the length of the gonotrophic cycle, or blood-digestion rate, as a function of temperature. Clearly, there is a need to determine which of these assumptions most closely approximates to reality. Whilst 'experimental' models are a useful first step for examining the inter-relationships between different variables, not enough is known about the simultaneous interactions of variables on different parts of the models for their predictions to be reliable. Moreover, many of the assumptions on which such models are based are difficult to quantify because of the many uncertainties surrounding them.

In the empirical approach to forecasting, attempts are made to identify the major environmental determinants which govern disease processes. This method is usually less expensive in time and money than the experimental approach, but it is possible only if there are large data sets describing vectors or disease incidence over time or space. This approach has been used to great effect in the past. In the Punjab, Christophers (1911) was able to show how rainfall was directly related to the number of deaths from malaria each year (see Fig. 5) [R^2 (adjusted)=44.5% and $P<0.001$, based on a re-analysis of the data for the period 1868–1908, excluding 1884, the data for which is missing, and 1868 and 1885, where there are no data for the previous year]. This work was extended by Gill (1928), who developed an accurate system for predicting epidemics at the district level. He showed that July–August

rainfall was a strong predictor of malaria deaths in October–November ($R^2=65.7\%$ and $P<0.001$, based on re-analysis of the data for 1868–1913). More recently, a simple relationship was found between the amount of malaria in different parts of Indonesia and annual temperatures and rainfall (Anon., 1994); the model used forecast that, although global warming would produce little immediate increase in malaria, the annual incidence of this disease would rise by around 25% by 2070.

A novel method for exploring the relationships between the risk of malaria and the environment at a local level has been the use of images from Earth-orbiting satellites for quantifying mosquito breeding sites in an area. For example, Beck *et al.* (1994) used an image from a satellite of the *Système Probatoire d'Observation de la Terre* to quantify the amount of wetland and rough pasture surrounding villages in Mexico and showed that they could use these features to predict villages at high or low risk for malaria transmission with an overall accuracy of 90%. Thomson *et al.* (1996) were able to demonstrate an empirical relationship between mosquito abundance, normalized difference vegetation indices (NDVI), cold-cloud duration and soil type in The Gambia, which they refer to as a relationship between malaria-transmission indicators and proxy environmental variables. These authors also suggest the relevance of various, remotely sensed variables to malaria transmission (e.g. the potential use of land-surface temperature as a proxy for ambient temperature, the use of NDVI away from coastal areas as an estimator of saturation deficit, and the use of day/night thermal differences as estimators of surface water). One deficiency in the empirical approach is that it may be very difficult to identify the reason for an incorrect prediction. Moreover, whilst it may be possible to predict the abundance of vectors in an area accurately by using environmental parameters, the relationship between vectors and disease may not be so transparent. In The Gambia, for example, an empirical approach showed that proximity to the river was a good predictor for the number of mosquitoes found in a village (Lindsay *et al.*, 1993). The risk of transmission

might therefore be expected to be greatest in the villages close to the river, which had most mosquitoes. However, the most malarious areas were those with fewest mosquitoes (Thomson *et al.*, 1994). This apparent paradox was explained by the habits of villagers: in general, only those sleeping in areas where mosquito densities were high slept under bed-nets. It is such idiosyncrasies in human behaviour and immunity which can make accurate predictions so difficult to obtain, particularly when studying small-scale variations in risk. Thus, it should be appreciated that the risk from malaria is not merely a function of environmental and ecological factors; these only establish whether transmission would be possible and hence whether there is a health hazard. The risk of disease depends on additional factors: the vulnerability of the human community and the capacity and capability of health-protection agencies (Birley, 1995). Human vulnerability is the product of immunity, poverty and behaviour. People can do much to protect themselves from malaria just as health services can do much to protect the community. The ability to respond appropriately is mostly dependent on economic, social and political factors which are outside the scope of this review.

Whilst models of malaria risk will be useful to health planners operating at a global level, it is important that these models are validated using historical or contemporary data sets. Moreover, there is an urgent need to go back to the basics and test the assumptions on which the models are based in a variety of settings, particularly in relation to the effects of temperature and relative humidity on the dynamics of transmission. To date, based on intuition, mathematical models and reports from the field, the most serious consequence of climatic change appears to be an increased likelihood of malaria epidemics in areas of fringe transmission, particularly in tropical highlands, where people have little or no immunity to this disease, are poor and are unprotected by health services. Health authorities in areas of unstable transmission need to be vigilant in order to detect changes in the distribution patterns of malaria and to respond appropriately when outbreaks occur.

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