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History of and prospects for mosquito-borne disease in Britain

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Abstract

Incidence of mosquito-borne disease in Britain has been strongly influenced by land use, human innovation and lifestyles affecting human-mosquito contact. Autochthonous malaria has not been detected for half a century despite high numbers of imported cases, especially since the early 1970s, and not a single human case of a mosquito-borne arbovirus has been detected for almost a century and a half. On the other hand, natural climatic fluctuation is increasingly affected by unprecedented use of fossil fuels since the early 19th century, with uncertain but appreciable rates of global warming set to continue into the foreseeable future, necessitating nationwide reorganisation and expansion of flood defence and urban drainage works. Though the probability of outbreaks of mosquito-borne disease may still be low, longer-term prospects are less certain. Many factors influencing transmission of mosquito-borne pathogens in Europe are imperfectly understood and there are important gaps in knowledge of the taxonomy, distribution, prevalence, bionomics and ecology of British and Northwest European mosquitoes. Resolution of these discrepancies is necessary for planning and execution of effective remedial measures if and when problems occur.

Introduction

Yellow Fever, transmitted by *Stegomyia aegypti* developing in on-board water containers in ships carrying infected crew and/or passengers arriving from the tropics and sub-tropics, and *vivax* malaria, considered to have been transmitted predominantly by *Anopheles atroparvus* in low-lying marshy situations, are the only mosquito-borne pathogens known to have been transmitted to humans in Britain (Snow, 1991; Ramsdale & Snow, 1995). Both had virtually disappeared, apparently spontaneously, when the vector role of mosquitoes was proven at the close of the nineteenth century. Their disappearance owed little to medical intervention[1], but was an unforeseen result of innovation in seemingly unconnected fields of human activity: advances in ship design in the case of Yellow Fever (Snow, 1991) and changes in farming practice allied to improving housing and hygiene, particularly separation of human and animal housing, in the case of malaria (Bruce Chwatt & de Zulueta, 1980; Dobson, 1997, 1998; Ramsdale & Snow, 1995; Hutchinson, 2004). Mosquitoes of the *Anopheles maculipennis* complex, including the principal northern European vector, *An. atroparvus*, habitually rest in occupied buildings providing a ready source of bloodmeals, and malaria transmission had been domestic.

Predicted future incidence of mosquito-borne disease has received much attention (e.g. Jetten *et al.*, 1996; Lindsay & Birley, 1996; Snow, 1999; Reiter, 2000, 2001; Rodgers *et al.*, 2001; Crook *et al.*, 2002; Kuhn *et al.*, 2003; and others), especially in relation to the influence of climate change which is expected to have wide-ranging economic and environmental consequences (King, 2002).

It is our intention to briefly review the incidence of mosquito-borne pathogens in this country during the twentieth century, and to examine ongoing man-driven environmental changes which influence inland and coastal flooding and drainage, and hence prevalence and distribution of mosquitoes and possible incidence of mosquito-borne diseases during the present century.

[1] Although quinine became increasingly available during the nineteenth century, its cost until its closing years was prohibitive (James 1929; Bruce Chwatt & de Zulueta, 1980). Even at its cheapest it must have been expensive for poor people with large families and it is uncertain to what extent quinine was preferred over patent wide spectrum palliatives. Ague, as was stressed by Hutchinson (2004), was a blanket term covering malaria and other feverish maladies. Dobson (1997, 1998) tells of the former use of opium as a remedy for ague and Marshall (1938) stated, "opium pills were sold for this purpose within living memory in Havant". Sallares (2002) goes on to tell of finds of the opium poppy (*Papaver somnifarum*) from Iron Age Roman archaeological sites in East Anglia, with the inference that it was grown for the same reason at this early date. What is clear is that incidental consequences of human innovation had a far greater impact on mosquito-borne pathogens in Britain than did medical intervention.

Climatic trends

Many different factors influence our current climate. In the geological past these may have included variation in solar output, oscillations in the earth's orbit and its axial tilt. Interactions between ocean and atmospheric systems can cause annual and centennial climatic variability on a global and regional scale. However, as reported by the Intergovernmental Panel on Climate Change (IPCC), warming experienced over the last century cannot entirely be explained by this natural variability.

Factors affecting global climate are referred to as positive or negative forcing agents. Positive forcing agents such as carbon dioxide, methane and nitrous oxides trap energy in the lower regions of the earth's atmosphere causing global temperatures to rise. Conversely, negative forcing agents such as sulphur dioxide and some soot particles such as those produced by volcanic eruptions, reduce the amount of solar energy reaching the earth's surface, thus cooling the atmosphere. Since the beginning of the 19th century, mainly as a result of fossil fuel burning, concentrations of positive forcing agents have increased (IPCC, 2001). This increase can be clearly seen in Figure 1.

The Hadley Centre, part of the United Kingdom Climate Impacts Programme (UKCIP) has developed models representing global climate change. When details of positive and negative forcing agents are put into these models, the results closely simulate the 0.6°C rise in global temperatures experienced up to the end of the 20th century.

The rate and amount of future climate change will be affected by current and future emissions of forcing agents and the degree to which the climate responds. The UKCIP02 climate change scenarios (Hulme *et al.*, 2002) are based on four different emissions scenarios developed by the Special Report on Emissions Scenarios (SRES) set up by the IPCC. These scenarios deal with the evolution of world culture, population, technology and economic development and seek to predict global annual carbon emissions. The UK Office of Science and Technology's (OST) description of these scenarios is summarised in Table 1, and annual carbon emissions are summarised in figure 2.

The emissions scenarios provide information to modellers about expected levels of forcing agents. This allows predictions to be made as to how the climate may respond to each scenario. The 'forecasts' are given for three thirty year time slices centred on the years 2020, 2050 and 2080. Once emitted the residual life of carbon dioxide in the atmosphere is 30-50 years. Humanity's response in reducing emissions will therefore have only a small effect on temperature until the carbon dioxide emitted to date has passed through the system. As a result there is little difference in predicted temperature changes between emissions scenarios until 2050.

Temperature change can be presented in a number of different ways, of which increases in summer temperatures (figure 3) and predicted increases in length of the thermal growing season are the most pertinent to vector activity. The growing season is already lengthening and may be up to 30 days longer if high emissions of forcing agents continue to 2020. Depending on emissions levels, predicted increases are 35-55 days by 2050 and of 50-100 days by 2080.

Responses to flood risk

Until the 1970s, flood defences were constructed to protect urban and rural areas from flooding and to raise agricultural productivity with land drainage schemes and grants. However, recent trends supported by new legislation (Water Resources Act, 1991) have tended toward flood risk management, including greater acceptance of rural flooding. Urban flood defence is given the highest priority and more emphasis is placed on habitat creation than on the protection of agriculture from flooding or the provision of land drainage. Assuming the nation remains able to depend upon imported food, the main driver of future flood risk management policy will be the need to respond to climate change. The Foresight Scenarios (Evans *et al.*, 2004) suggest that as a result of climate change the number of people exposed to flood risk may rise from 1.5 million to 3.5 million. Annual flood damage could rise from the present level of £1 billion to about £25 billion in the worst case scenario.

As climate change increases the volume of seawater by thermal expansion, and as polar and glacial ice melts, sea level is rising by 3mm per annum. During the last glacial period the weight of the ice sheet caused the southern parts of the UK to rise and the north to sink. At the end of this ice age the retreat of the ice sheet allowed the land to return toward its original position in the north of the UK. However, this 'isostatic rebound' is causing land levels in the South East to sink by 3mm per annum. This reduces the relative rate of sea level rise in the north but increases the relative rise to a total of 6mm per annum in the South East. In addition, increased storminess is likely to result in more severe and frequent tidal surges and some increase in wave height.

Coastal flood defence managers use walls to prevent tidal inundation, but also rely upon the foreshore to dissipate wave energy, prevent damage to walls and wave overtopping. As it is appreciated that it is not possible to hold back the sea in all circumstances, acceptance of the need to abandon some tidal defences is growing. Additionally, designated habitats benefiting from statutory protection may be squeezed out of existence between defences and the rising sea. Tidal flood defence lines may be legally required to move inshore to preserve these habitats. An example of this is taking place at Abbots Hall in Essex where defences have been breached and new salt marsh habitat encouraged. Nationally, it is also possible that defences may be more frequently overtopped causing freshwater marshes to become more brackish.

Predictions of winter precipitation are more uncertain than those relating to sea level rise; consequently changes in fluvial flood flow are far harder to estimate. Current guidance from the centre of Ecology and Hydrology (Reynard *et al.*, 1999) is that flood flows may increase by as much as 20% by 2050. Depending upon location in the UK, it is expected that this may result in a flood expected on average once every hundred years to occur once in every forty years.

As fluvial flood mechanisms are more complex than those of tidal flooding, the suite of tools available for their management is more diverse. As in coastal defence management, walls or embankments may be employed to protect areas from inundation. River conveyance capacity may be altered to hasten or delay flood flows. This option is likely to be pursued in conjunction with the creation of engineered or more natural washlands. The aim of these washlands is to store excess flow for release when the peak of a flood has passed, dampening the response of the catchment and reducing peak flows. To maximise flood storage volume these washlands would need to be emptied as quickly and completely as possible. Given that agricultural subsidies will no longer be paid according to production, but for achieving environmental outcomes, it is likely that fluvial floodplains will in some areas return to a more natural marshy state. Nature conservation bodies (English Nature, the RSPB, the National Trust and local nature trusts) expect these floodplains to provide new wildlife refuges.

Exceptionally intense rainfall events expected on average once every two years are predicted to have increased by 20% by the year 2080 (Hulme *et al.*, 2002). It follows that pluvial flooding, caused by rainfall exceeding the design capacity of urban drainage systems, will also increase. Urban drainage systems typically offer a fairly low standard of defence, and in older developed areas, surface water drainage systems are often connected to the foul water system. The need to upgrade these systems will therefore be pressing but, as they are buried below ground, expensive. It is possible that retrofitting storage tanks to piped subsurface systems will offer a cheaper answer than re-laying entire networks. However, design must aim at precluding breeding of hypogeal urban mosquitoes, especially of the anthropophilic (*molestus*) biotype of *Culex pipiens*.

Incidence of mosquito-borne pathogens in Britain during the twentieth century

Rural housing continued to improve throughout the twentieth century. Double storied dwellings now outnumber single storied structures, though even these are too light and airy to provide endophilic mosquitoes with suitable harbourages. Because of almost universally installed central heating, human habitations are now too desiccating for survival of overwintering *An. atroparvus.* Odour plumes used by foraging mosquitoes for host location now emanate primarily from ground level animal housing. The much weaker plumes flowing from the dwellings of today's smaller families are usually from upstairs windows of bedrooms occupied by no more than one or two people.

Nevertheless, there is documentary evidence of two occasions of people housed in crowded ground level accommodation in the north Kent marshes being attacked by *An. atroparvus* (Ramsdale & Snow, 1995). On the first occasion, servicemen repatriated from malarious theatres during the 1914-1918 war were lodged in sub-surface or ground level fortifications and huts on the Isles of Grain and Sheppey, where *An. atroparvus* was abundant. This situation provided the mosquito with attractive resting sites containing concentrations of suitable hosts, some of them carriers of *Plasmodium vivax*, and led to the only epidemic of malaria in Britain since the disease disappeared towards the end of the 19th century (Shute, 1963). It also accounted for 85% of the malaria occurring in Britain during and immediately after the 1914 -1918 war. Potential relapsing cases were not posted to receptive areas during the 1939–1945 war and, of a total of 34 indigenous cases reported in the whole country between 1941 and 1948, only 26% were in the Thames estuary counties of Kent and Essex (Shute, 1949; Shute & Maryon, 1974). The second incidence of attack was when the large labour force assembled for construction of the Grain Power Station in the early 1950s was housed in temporary huts on the edge of Grain marshes, creating a situation resembling the military encampments of 1914-1918. Large numbers of bloodfed *An. atroparvus* were collected from these huts throughout this occupation (Shute, 1951). During this period the great storm surge of January 15th 1953 inundated large areas of eastern England, resulting in great damage and loss of life. The flooding was long lasting with much low-lying coastal and estuarine land south of Flamborough Head under water for months, and with damage necessitating construction of more substantial and continuous sea defences. The malaria situation at Grain was closely monitored, but this time there were no parasite carriers and no local transmission (Shute, 1952, 1953).

Only a handful of autochthonous cases were recorded after 1948; all *vivax* infections during the 1950s (Bruce Chwatt & de Zulueta, 1980; Bradley, 1989). Two of these were in the London Borough of Lambeth, and are thought to have been transmitted by urban *An. plumbeus* (Shute, 1954). Two cases of *falciparum* malaria considered to have been transmitted by an imported exotic, already infective mosquito occurred almost simultaneously near Gatwick Airport in 1983 (Whitfield *et al.*, 1984; Curtis & White, 1985). *Anopheles atroparvus* is refractory to infection with extant strains of *P. falciparum* (James *et al.*, 1932; Shute, 1940; Ramsdale & Coluzzi, 1975; Dashkova, & Rosnicyn. 1982; Ribeiro *et al.*, 1989), though *An. plumbeus* appears to be a potential vector (Blacklock & Carter, 1920; Blacklock, 1921; Marchant *et al.*, 1998; Eling *et al.*, 2003). Other instances of "airport malaria" have occurred elsewhere in Europe and have included some deaths (Gratz, 2004) but, as in the UK, these are infrequent and have not led to secondary cases.

Large numbers of imported malaria cases were detected during the latter half of the century (Bradley, 1989; 1993), more than in any other European country except France, where over twice as many were reported (Gratz, 2004). Incidence of imported malaria in Britain increased annually from 1970 to reach over 2000 cases in 1979, after which it remained at a high level. Until the late 1980s imported cases were predominantly of *vivax* malaria coming from southern Asia where the disease was resurgent (WHO, 1979). This resurgent malaria was brought under control during the late 1970s and early 1980s, and in 1988, for the first time, the number of *falciparum* cases imported into Britain exceeded those of *vivax* malaria, since when *P. falciparum* has continued to be the principal cause of imported malaria. Examination of the origins of imported cases of *falciparum* malaria in 1988 showed that about 94% were acquired in Africa (Bradley, 1989). Because of drug resistance it is a disease particularly worrying for clinicians and within the decade 1989-1999, 680 people died from *P. falciparum* infections imported into the WHO European Region (Gratz, 2004).

Analysis of the cases of imported *falciparum* malaria in the 1980s showed that new immigrants accounted for only 4%, but settled immigrants returning from visits to their countries of origin, or visitors to friends or relatives in Britain accounted for 61%. However, as Bradley (1989) pointed out, numbers of cases of imported malaria in different categories of people entering this country fluctuates with wars and civil disruptions in different regions. Although there is no information on the personal circumstances of immigrants and visitors from Africa, probably most are urban dwellers.

Britain appeared to be almost free of mosquito-borne viruses affecting humans, other mammals or birds throughout the twentieth century, except for outbreaks of myxomatosis in tame and wild rabbits, of which many western European mosquitoes are proven or probable vectors[2] (Muirhead Thompson, 1956a, 1956b; Service, 1972). The myxoma virus was isolated from adult female *Culiseta annulata* collected in France during the winter by Gilot *et al.* (1979), who suggested that this mosquito and the flea (*Spilopsyllus cuniculi*) may act as winter reservoirs of the virus. *Culiseta annulata* overwinters without recourse to diapause, feeding during the winter whenever warmer periods allow (Ramsdale & Wilkes, 1984).

[2] The myxoma virus does not replicate within arthropod vectors and transmission was at first regarded as a simple mechanical transfer of virus particles on contaminated mouthparts during interrupted bloodmeals (Bates, 1949). However, some viruses can persist for extended periods in insects, including mosquitoes, and still be transmitted. Myxoma transmission seems to be of the non-circulative type (i.e. without invasion of cells and replication in the arthropod host) widely employed by plant viruses, but also by some animal viruses (Gray & Bannerjee, 1999). Occasional non-circulative transmission by many mosquito species of other pathogens, including the usually tick-borne Omsk Haemorrhagic Fever, Lymphocytic Haemorrhagic Fever and the bacterium *Francisella tularense* have also been reported in Scandinavia and/or eastern Europe (Olin, 1942; Gagarina & Netskii, 1955; Gutsevich *et al.*, 1971; Goplas, 1974; Carn, 1999).

The single record of antibodies to an arbovirus was of Tahyna (Bunyaviridae) in the rodents *Apodemus sylvaticus* and *Clethrionomys glareolus* in Devon (Chastel *et al.*, 1985). This and other arboviruses of the Togaviridae, Flaviviridae and Bunyaviridae are prevalent and widespread in continental Europe as far north as Scandinavia, and involve widespread human infections. These viruses are regularly brought to Europe by migratory birds (WHO, 1985) and their apparent absence from Britain was always difficult to explain. Then, in the opening years of this century, Buckley *et al.* (2003) demonstrated the presence of Sindbis (Togaviridae), Usutu and West Nile (Flaviviridae) in migratory and resident birds exhibiting immune responses indicative of long exposure to these viruses, with the inference that avian transmission cycles in this country are of long standing.

The short term twenty-first century outlook

The question of malaria becoming a problem again is confined to *vivax* infections (de Zulueta *et al.*, 1975) and is concerned with the chances of what Macdonald (1957) termed epidemics starting from small beginnings in non-immune societies. The original case(s) would most probably be undetected asymptomatic parasite carriers protected from clinical effects of the disease by an immunity acquired and maintained in an area where malaria is endemic. On the other hand, secondary cases would almost certainly be non-immunes exhibiting the classical symptoms of malaria. Diagnosis is straight forward, and even in rural areas, prompt curative treatment would quickly eliminate these new sources of infection to mosquitoes. Even with a substantial amount of man-biting by potential vector mosquitoes, it would be improbable that an epidemic would occur in a non-immune human population covered by an efficient health service alive to the possibility of malaria[3]. The fact that *An. atroparvus* now seldom comes into contact with man makes the possibility of a malaria epidemic under present conditions remote. Most people are urban dwellers more likely to encounter *An. plumbeus*, but this species was incriminated only four times in Britain during the twentieth century. The southern European countries are still free of epidemic malaria, though a few sporadic cases have been reported in recent years (Gratz, 2004).

There is insufficient evidence on which to base a realistic assessment of the risks of outbreaks of mosquito-borne arboviral infections in humans or domestic animals.

Longer term prospects.

Longer term risks of mosquito-borne disease transmission will be strongly influenced by continuing climatic warming and by environmental changes brought about by the coastal and inland flood defence works described earlier. The possibility of future outbreaks of malaria or one or more arboviral diseases in the different conditions forecast for later in the century cannot be dismissed.

Some other mosquito-borne pathogens in Europe may also have to be considered in the longer term. These include *Dirofilaria immitis* and *D. repens,* causal organisms of heartworm in dogs and cats (Bain, 1978; Cancrini. & Accardi, 1980; Canastri-Troth *et al.*, 1988; Aranda *et al.*, 1998). Aberrant *Dirofilaria* infections in man are associated with lesions in the lungs, subcutaneous tissues and the eye (WHO, 1979). In the insect the minimum period to infective stage larva (L3) is 18-20 days at 22°C. Stage L3 is not reached at temperatures of < 18°C but larvae remain alive and resume development if temperature temporarily rises (Cancrini *et al.*, 1988). Other filariae of the genera *Dipetalonema, Dirofilaria, Mansonella, Setaria* and *Foleyella,* are transmitted to a variety of wildlife and domesticated animals in eastern and southern Europe (Gutsevich *et al.*, 1971).

The immediate concern must be whether or not in the event of an outbreak of one or more mosquito-borne diseases it would be possible to apply effective remedial measures based on extant knowledge.

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[3] All malaria cases (imported or autochthonous) in the UK and Western Europe can get effective treatment when they feel ill, so very few develop gametocytes which could infect mosquitoes. This contrasts with (a) diseases with animal reservoirs and (b) malaria in former Soviet Central Asia and the USA where lack of universal health services leaves poor people unable to get their malaria treated and who, therefore, are likely to infect mosquitoes. (This was well brought out in a recent BBC4 malaria film which reported on autochthonous cases in Palm Beach, Florida thought to originate from homeless Latin American immigrants living rough, but leading to better-off Americans getting malaria and having to pay to go to hospital with it). Thus risks of vector-borne diseases returning are not just about biology of vectors and parasites in relation to temperatures, but also the politics of health care.

Summary of present knowledge

1. Mosquito-borne diseases

Ambient temperatures in Britain are currently no more than marginally suitable for completion of extrinsic development of *P. vivax* (Table 2). As is made plain by the writings of Shakespeare, Defoe and others this was formerly transmitted even in the colder (little ice age) climate of the 16th to 18th centuries (Crossfil, 1952; Raper *et al.*, 1997; Reiter, 2001). However this was only because the endophilic *An. maculipennis* complex (principally *An. atroparvus*, possibly also *An. messeae* and/or *An. daciae*) escaped exposure to diurnal temperature minima. Predictions of progressive increases of ambient temperatures during the twenty-first century, in addition to extension of the season and areas in which transmission of mosquito-borne disease is possible, may also permit the exophilic *An. claviger, An. algeriensis* and *An. plumbeus* to become malaria vectors, particularly if climatic amelioration leads to a greater demand for outdoor activities and waterside amenities provided by a growing leisure industry. Laboratory observations in Britain and France found that *P. vivax* may remain viable in the mosquito for 80 days (James, 1920), and even as long as 127 days (Roubaud, 1918).

Incidence of mosquito-borne arboviruses in Europe was reviewed by Lundström (1999), since when Usutu virus, detected in Europe late in 2001 during an investigation of deaths from encephalitis of blackbirds (*Turdus merula*), swallows (*Hirunda rustica*) (presumably recently fledged) and owls (*Strix nebulosa*) near Vienna, has been added (Table 3). This represented the first record of Usutu virus north of the Sahara, and evident absence of immunity in resident Austrian birds (Weissenböck *et al.*, 2002) contrasted with the situation in England, mentioned earlier. South of the Sahara, where Usutu virus is widely distributed, it is transmitted between birds by ornithophilic mosquitoes, with only two records from mammals, from a soft furred rat (*Praomys* spp.) and from a man with fever and a rash (Karabatsos, 1985; Adam & Diguette, cited by Weissenbock *et al.*, 2002). Neither Usutu, nor the infrequently recorded Lednice virus (Bunyaviridae) have yet been isolated from humans in Europe. Lednice has only been detected in *Cx. modestus* in the Czech-Slovak border area (Malkova *et al.*, 1974) and in ground nesting water birds in Romania (Draganescu *et al.*, 1981). Antibodies to Semliki Forest and/or Chikungunya viruses in humans, bovids and ovids have been found in southern Europe and Austria, and in birds (Passeriformes) in Austria (Lundström, 1999). However, the finding of antibodies to Semliki Forest virus in serum from an overwintering, but northern European nesting, Red throated Diver (Gaviiformes) in Romania, may indicate a wider distribution. Molnar *et al.* (1979) reported antibodies of the Uukuniemi A and B subgroups (Phleboviridae) in sera from apparently healthy people and cattle in Hungary. As yet this is a unique record despite searches elsewhere in Europe (Lvov *et al.*, 1989). There are records of Toscana Sandfly Fever, usually transmitted by *Phlebotomus perniciosus*, in *An. claviger* and *Cx. pipiens* in Italy (Sabatinelli *et al.*, 1981), whilst Hurlot & Thomas (1960) showed that the related Sicilian Sandfly Fever replicates in *Cx. tarsalis* and *Cx. univittatus.* Some Phleboviruses are principally mosquito-borne. Notable amongst these is Rift Valley Fever, endemic in Africa as far north as Egypt, where both humans and livestock are affected.

Mosquito-borne arboviruses typically circulate in feral bird or mammal–mosquito cycles and human involvement follows intrusion into these ecosystems (Jupp & McIntosh, 1988; Gray & Bannerjee, 1999). The bird associated Sindbis group and West Nile viruses and the mammal associated Batai and Tahyna viruses are responsible for periodic human outbreaks of varying severity in Europe. Arbovirus circulation is not confined to southern Europe and human outbreaks of the Sindbis related Ockelbo viruses are frequent in Scandinavia and northern Russia (Lundström, 1999). Although human illness is not observed, antibodies to Inkoo virus are common in northern Fennoscandia, where transmission is both intensive and extensive, with high infection rates in domestic and wild herd animals (bovids up to 88% and reindeer (*Rangifer tareandi*) 89%) (Brummer-Korvenkontio, 1973; 1974; Snow, 1991).

Batai, Sindbis-like, Tahyna and Inkoo viruses have all been found at latitudes higher than 60°N in Europe (Snow, 1991) and isolates of Ockelbo have been obtained from within the Arctic Circle (Mitchell *et al.*, 1993). High incidence of Tahyna virus in sera from humans (52.7%), reindeer (85.2%), and cattle (66.6-79.9%) is found in the north-western Russian Plain (Lvov *et al.*, 1989). Snowshoe hare and Lumba-related viruses (Bunyaviridae, California Encephalitis Group) and Getah virus (Alphaviridae), have been additionally reported from western Siberia (Mitchell *et al.*, 1993). West Nile virus has been found at about 50°N in North America (Higgs *et al.*, 2004) and continental Europe (in *Ochlerotatus cantans*) (Labuda *et al.*, 1974), and at 52°N in Britain in infected resident birds (Buckley *et al.*, 2003).

The role of vertical (transovarian) transmission in arthropod vectors in virus persistence in seasonally hostile environments is well established (Reeves, 1974, 1987; WHO, 1985). A report of Sindbis antibodies in overwintering Whitefronted Geese (*Anser albifrons*) in Romania (Draganescu *et al.*, 1978) suggests that transmission from and to vertebrates may also occur near or within the Arctic, where several Anseriformes, Gaviiformes and Charadriiformes habitually nest. These birds migrate along coastlines or waterways to areas where water remains unfrozen. Unlike the north–south direction of the trans-Saharan migrations, seasonal movements of these and some other Charadriiformes, Columbiformes and Passeriformes are in more or less east–west directions, an aspect of possible Eurasian transportation of arboviruses meriting further attention.

Avian roosting behaviour may be important in transfer of viruses from birds to mammals. Waders and other birds nesting and roosting at or near ground level may be more vulnerable to attack by foraging mammal oriented mosquitoes, which may act as both bridge and epizootic or epidemic vectors of the bird oriented West Nile and Sindbis-like viruses. Whilst promiscuous host choice may not be suited to the maintenance of a stable virus reservoir, it may be of importance in promoting epidemics or the initiation of new transmission cycles (Mattingly, 1960). Conversely, Batai, Inkoo, Tahyna and Chikungunya viruses, normally maintained in mammal associated transmission cycles may be transmitted to ground level nesting birds as a step to a more general avian cycle important in long and short range expansion of their distributions.

Birds are not the only means of international transport open to arboviruses. Dengue (types I, II, III and IV) is re-appearing as an emerging imported disease in European travellers returning from tropical and sub-tropical countries (Jelinek *et al.*, 2002), becoming the most common imported mosquito-borne disease in Sweden (Lindbeck *et al.*, 2003) and second only to malaria in Germany (Frank *et al.*, 2004), though the only fatal cases have occurred in Britain (2) and Finland (1) (TropNetEurope, 2003). The volume of international travel has increased dramatically during the past half century and the upward trend seems destined to continue into the foreseeable future. Before eradication from the continent by the DDT spraying campaigns of the 1940s and 1950s, *Stegomyia aegypti* was on the edge of its distribution in southern Europe and both Yellow Fever and Dengue were epidemic. There is not enough information on extrinsic temperature requirements of these viruses, or on whether they could adapt to temperate climate vectors. . Roubaud *et al.* (1937) demonstrated that *Oc. geniculatus* is capable of transmitting Yellow Fever almost seventy years ago.

Arboviruses have been isolated from each of six of the seven mosquito genera recorded in Britain, with insufficient information to either include or exclude the genus *Orthopodomyia* from the list of potential vectors. Host preferences, species abundance and phenology may be the most important factors determining vector roles. In this respect, establishment of *Stegomyia albopicta* in parts of continental Europe may assume greater importance with continuing climatic amelioration. With increasing latitude the length of the extrinsic incubation period of the virus and gonotrophic cycle of the mosquito assume greater importance (Turell & Lundström, 1990; Blair *et al.*, 2000). However, the few available data on extrinsic incubation present a confused picture, with negative as well as positive temperature relationships reported (Kremer *et al.*, 1983).

Quite recently Higgs *et al.* (2005) discovered high rates of "nonveremic" transmission of West Nile Virus from infected to uninfected mosquitoes co-feeding on uninfected vertebrates. It seems that when feeding in close proximity non-infected mosquitoes may acquire virus particles deposited on the skin or fur of the vertebrate by probing infective mosquitoes, the vertebrate merely acting as a virus transfer platform. It is not known how long the virus particles remain viable, but nonviremic transmission between insect vectors clearly differs from the non-circulatory mode of transmission adopted by the Myxoma Virus (see footnote 2). Discussing this discovery, the authors point out that, amongst other implications, even immune, or non-susceptible, or supposedly dead-end vertebrates may facilitate mosquito infection, thereby acting as so-called amplifying hosts, which might partially explain the rapid dispersal of West Nile Virus in North America. As far as this summary of present knowledge is concerned, it emphasizes our imperfect, even rudimentary, understanding of arbovirus epidemiology.

2. Mosquitoes

Knowledge of the mosquito fauna of Britain stems from information gathered by many sources. The current checklist and distribution charts include 33 species contained in seven genera: *Anopheles* (6) *Aedes* (2), *Ochlerotatus* (12), *Coquillettidia* (1) *Culex* (4), *Culiseta* (7) and *Orthopodomyia* (1) (Cranston *et al.*, 1987, Snow, 1990; Snow *et al.*, 1998; Linton *et al.*, 2005), but only some of these are widespread or abundant enough to be regarded as incontrovertibly endemic. Of the species rarely recorded in this country *Culex modestus*, found twice, in 1944 and 1945 near Portsmouth, is primarily a southern Palaearctic species, but occurs along the western seaboard of France as far north as the mouth of the Loire (Moussiegt, 1986). These wartime records may represent importation by ship or aircraft, the only modes of international transport then available. *Aedes vexans*, recorded fifteen times in more than a century following the first listing by Verrall (I888), *Oc. communis*, recorded four times (including a record from Jersey) since 1922, *Oc. dorsalis*, recorded on fifteen occasions (Dorset to Thames Estuary and North Wales) between 1919 and 1995, *Oc. leucomelas,* recorded once (Nottinghamshire) in 1919, *Oc. sticticus*, recorded on five occasions (Hampshire to Perthshire) between I827 and 1910 and not since, and *Cs. longiareolata,* found three times (near Portsmouth in 1940, Epsom in 1953 and Poole in 1969) (Snow *et al.*, 1998), are all endemic to north-west Europe (Becker *et al.*, 2003) and British records may represent occasional importations. On the other hand, as many parts of Britain have never been explored and some species records represent fortuitous discoveries not followed up, some or all may be endemic.

Considerable taxonomic advance has been made since most of the native species were recorded. Major revision of the classification of the tribe Aedini, not yet finalized, is leading to recognition of new genera and subgenera world-wide, including Europe (Reinert, 2000; Reinert & Harbach, 2005). At the same time, DNA sequencing is revealing the existence in Europe of hitherto undescribed species in the holarctic *Anopheles maculipennis* group (Sedhagat *et al.*, 2003, Nicolescu *et al.*, 2004). One of these, *An. daciae*, has been collected in the Somerset Levels (Linton *et al.*, 2005) and may prove to have a wider distribution. Re-examinations of the taxon *Aedes cinereus*, first listed by Verrall (1888) and widely distributed here, led to the recognition of the sibling species, *Ae. geminus* by Peus (1970) and *Ae. rossicus* by Gornostaeva (2003), both with wide European distributions. *Aedes geminus,* more abundant than *Ae. cinereus* in France (Schaffner & Pfirsch, 1995), is considered by Becker *et al,* (2003) to be present in Britain. The full extent of the distribution of *Ae. rossicus* is not fully known, but probably ranges from eastern Siberia to the Atlantic (Becker *et al.*, 2003).

Morphological separation of some *Ochlerotatus* species is difficult and may affect understanding of distribution and ecology. Over a two year trial period in Denmark specimens taken from natural, mixed *Oc. annulipes/Oc. cantans* populations were identified morphologically using British, German and Russian keys. Concurrent allozyme electrophoresis revealed up to 27% of morphological misidentifications in different samples, and further revealed the unsuspected presence of a third species, *Oc. excrucians* (Overgaard Nielsen *et al.*, 1995). The overall situation regarding difficulties of morphological differentiation was further complicated when Arnaud *et al.* (1976) resurrected the taxon *surcoufi* from synonymy with *excrucians* and considered it to be the sole representative of the "*excrucians* complex" in France. Early records of *Oc. leucomelas* in eastern France were re-classified as *Oc. cataphylla* (Roman, 1958), though Schaffner (1998) states that *Oc. leucomelas* may be present in the north-east of the country, all of which raises doubts about the true identity of some records in Britain. Table 4 illustrates the current state of our knowledge.

The ubiquitous *Cx. pipiens* is probably the most important arbovirus vector in Europe, with the nominate biotype maintaining feral avian virus circulations and the *molestus* biotype transmitting to and between humans in urban and peri-urban situations. Fonseca *et al.* (2004) explain the greater current incidence of West Nile viral infections in North America by enhanced vectorial efficiency of hybrids between the two biotypes there, stating that hybrids are not found in Europe. However, some gene flow between urban (*molestus*) and rural (nominate) biotypes has been recorded in Europe (Urbanelli *et al.*, 1980) and the situation in parts of North America is complicated by the additional presence of *Cx. quinquefasciatus* with a reported hybrid zone drifting north and south according to periodic climatic fluctuations (Urbanelli *et al.*, 1997). A different approach is being pursued in northern Russia, where segregation due to behavioural differences is reported to be due to cytoplasmic incompatibility associated with the heritable, endosymbiotic bacterium *Wolbachia pipientis* (Vinogradova *et al.*, 2004). In yet another approach it is planned to apply methods developed in an investigation of the degrees of endophily and host specificity exhibited by individuals of the *An. culicifacies* complex in Sri Lanka (Rawlings & Curtis, 1982) to *Cx. pipiens* (C. Curtis, personal communication).

Early work on mosquito phenology, larval ecology and adult behaviour, summarised by Marshall (1938), gave a solid base for further studies. Since then sampling techniques for ecological and biological studies were described and discussed by Service (1993) and a great deal of information has accrued on many aspects of larval and adult biology. Relevant to vector roles was work on host preferences and times and heights of foraging, particularly as affected by meteorological conditions (e.g. Service, 1968, 1971a, 1971b, 1971c, 1971d, 1973, 1977, 1994; Packer & Corbet, 1994;

Birley & Charlwood, 1989; Renshaw *et al.*, 1995). Further data on host choice and vertical distribution of foraging mosquitoes has been gathered in Sweden (e.g. Jaenson, 1990; Lundström *et al.*, 1996). However, there is the need for more information on factors affecting hosts of differently situated populations, particularly of the saltmarsh *Oc. detritus*, responsible for the preponderance of pest mosquito complaints in Britain. Host preferences of many British mosquitoes are imperfectly understood, and often classified simply as man biting or not. Proper understanding of the maintenance of feral bird or mammal circulation of arboviruses demands a more detailed knowledge of this and other aspects of mosquito behaviour.

Conclusions

Though Britain may become increasingly receptive to a number of mosquito-borne pathogens during this century, the occurrence of epidemic malaria during the next several years is improbable. The disease is notifiable and the Malaria Reference Laboratory makes information available. On the other hand, the silent nature of many arbovirus infections makes effective notification impractical. Sindbis (Alphaviridae), Tahyna (Bunyaviridae) Usutu and West Nile (Flaviviridae) viruses have now been found in wild life in Britain. Of these, only West Nile virus is currently causing concern, but there appear to be mixed views on what preventive action, if any, is advisable or even possible (Crook *et al.*, 2002; Sharp, 2003; Donaldson, 2004).

Past and current apparent freedom of humans from mosquito-borne diseases may suggest low or negligible risk. On the other hand, although arboviral diseases may involve haemorrhagic fever and/or encephilitis, their presence may remain unreported or undiagnosed (Snow, 1991; Higgs *et al.*, 2004) until a major outbreak appears. Moreover, possible implications of the unknown aetiology of 60% of deaths from viral encephalitis over a nine year period (1989-1998) (Davison *et al.*, 2003) lends a certain urgency to the requirement of more information on arbovirus and potential vector prevalence and ecology.

It would be no more than prudent to take a closer look at the different elements involved in the dissemination of all mosquito-borne diseases and to attempt to fill existing gaps in our knowledge. Important will be more detailed and up-to-date information on mosquito prevalence and behaviour, as will be monitoring of environmental changes brought about by ongoing climatic amelioration, long term coastal and inland flood defence works, restoration of wildlife refuges and creation of outdoor amenities. Effective preventive or remedial action depends on informed, detailed comprehension of all relevant factors.

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Table 1. Summary of Future Emissions Scenarios (OST, 2004)

OST Scenario	Description	SRES Scenario	UKCIP02 Climate Change Scenario
World Markets	High national and global growth, with no action taken to limit emissions. Price of fossil fuels may drive development of alternatives.	A1F1	High Emissions
National Enterprise	Medium to low growth, no action taken to limit emissions. Increasing and unregulated emissions from newly industrialised countries.	A2	Medium High Emissions
Local Stewardship	Low growth, low consumption. However, less effective international action. Low innovation.	B2	Medium Low Emissions
Global Sustainability	Medium-high growth. High emphasis on international action to reduce emissions, coupled with innovation of new and renewable energy sources.	B1	Low Emissions

Table 2. Mean monthly temperatures recorded at three British localities (Pearce & Smith, 1993) and (in brackets) approximate duration in days of the extrinsic cycle of *P. vivax* (Pampana, 1963)

Month	London	York	Edinburgh
May	12.5°C (in)	11.5°C (in)	10.0°C (in)
June	16.0°C (55)	14.5°C (in)	13.0°C (in)
July	18.0°C (29)	16.5°C (45)	14.5°C (in)
August	17.0°C (38)	16.5°C (45)	14.5°C (in)
September	15.0°C (in)	14.0°C (in)	12.5°C (in)
October	11.0°C (in)	10.5°C (in)	9.5°C (in)

(in = indefinitely retarded)

Table 3. Arboviruses currently known to circulate in Europe

COMPLEX OR GROUP	VIRUS	HOST ORIENTATION	SEVERE HUMAN MANIFESTATIONS
ALPHAVIRUSES			
Western Equine Encephalitis Complex	**N. Europe (Ockelbo*)**	**Bird**	**Persisting arthralgia**
	Rest of Europe (Sindbis/Sindbis-like)	**Bird**	**arthralgia**
Semliki Forest Complex	**Semliki Forest Virus**	**Bird**	**arthralgia**
	ChikungunyaVirus	**Mammal**	**arthralgia**
FLAVIVIRUSES			
JapaneseEncephalitis Group	**West Nile Virus**	**Bird**	**Haemorrhagic Fever**
	Usutu Virus	**Bird**	**?**
BUNYAVIRUSES			
Bunyamwera Complex	**Batai Virus**	**Mammal**	**Malaria-like Fever**
California Encephalitis Group	**Tahyna Virus**	**Mammal**	**encephalitis**
	Inkoo Virus	**Mammal**	**encephalitis**

***Sindbis-like virus affecting humans in Norway, Sweden (as Ockelbo), Finland (as Pogosta) and Russia (as Karelian Fever)**

Table 4. Lists of endemic and rare mosquitoes in Britain, together with some potential North West European immigrant species

ENDEMIC MOSQUITOES	
Anopheles	*algeriensis; atroparvus; claviger; daceae; messeae; plumbeus*
Aedes	*cinereus*
Ochlerotatus	*annulipes; cantans; caspius; detritus; flavescens; geniculatus; punctor; rusticus*
Coquellettidia	*richiardii*
Culex	*europaeus; pipiens* (including nominate and *molestus* biotypes); *torrentium*
Culiseta	*alaskaensis; annulata; subochrea; fumipennis; litorea; morsitans*
Orthopodomyia	*pulcripalpis*
ADDITIONAL SPECIES RARELY RECORDED IN BRITAIN	
Aedes	*vexans*
Ochlerotatus	*communis; dorsalis; leucomelas; sticticus*
Culex	*modestus*
Culiseta	*longiareolata*
SOME POTENTIAL IMMIGRANT N.W. EUROPEAN SPECIES	
Anopheles	*maculipennis* sensu stricto
Aedes	*geminus; rossicus*
Stegomyia	*albopicta*
Ochlerotatus	*cataphylla; excrucians; japonicus; nigrinus; surcoufi*
Culex	*hortensis*

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History of and prospects for mosquito-borne disease in Britain

Figure 1. Rising atmospheric carbon dioxide concentration, 800 AD to 2000 AD (IPCC)

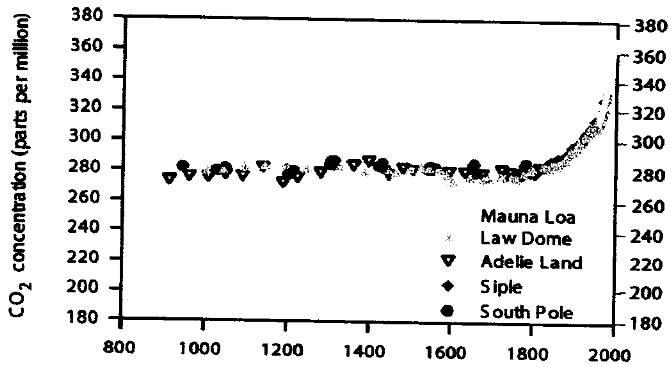

Figure 2. Global carbon emissions from all sources (SRES, 2000)

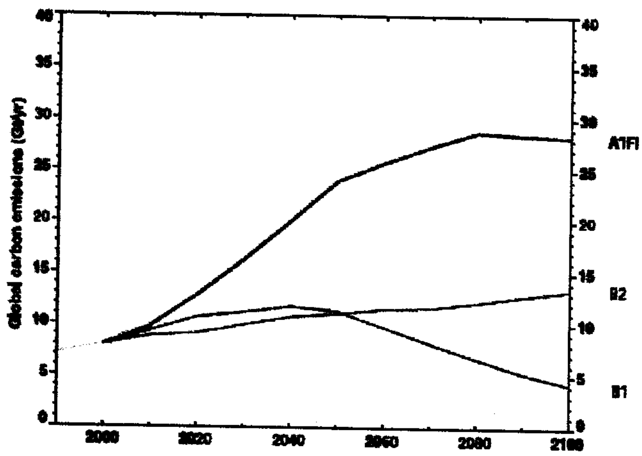

Figure 3. Predicted mean summer temperature changes in different emission scenarios