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Assessing the possible implications of wetland expansion and management on mosquitoes in Britain

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ABSTRACT

The expansion of existing wetlands, their creation from arable land, and the creation of new salt-marsh to alleviate coastal erosion and flooding are important UK issues as the environment sector adapts to the possible impacts of climate change and continues to meet its goals in providing increased wetland habitat for wildlife, and an outdoor space for human 'well-being'. Concerns have been raised over the potential impacts that such initiatives might have on mosquitoes and the possible future transmission of infectious diseases. This paper aims to firstly review wetland management and design strategies used in North America and Australia in relation to managing mosquitoes in wetlands, and secondly specifically discuss possible mitigating strategies for the key British mosquito species of freshwater wetland habitats in order to guide future research in this field. Developing this evidence-base is a crucial element in preparing for the emergence of mosquito-borne disease in the UK and in aiding policy makers in their assessments of the risks and impacts associated with wetland expansion on mosquito nuisance and disease risk. It is important to ensure that biodiversity gain and habitat restoration can advance without inadvertently elevating the risks from disease vectors.

Keywords: mosquitoes, wetlands, arbovirus, ecology, mitigation, UK

The Wetland Vision for England (Hume, 2008) outlines exciting plans to restore existing wetlands and create new wetlands from areas currently under agriculture. This is an attempt to provide an increased resource for biodiversity, assist with alleviating coastal and inland flooding and re-connect extant nature reserves to ensure that wildlife species are able to adapt to the impact of climate change. Currently there is no published research on the impacts of large-scale wetland creation/expansion programmes on the survival and abundance of mosquitoes in Britain and their ability to re-colonise former distributions or on the consequences that such a change might have on the transmission of mosquito-borne disease. A total of 34 species of mosquito (Diptera: Culicidae) have been recorded in the UK (Medlock & Snow, 2008a; Medlock & Vaux, 2009a) and the most common species are listed in Table 1 by dominant habitat.

It is vital that wetland creation schemes take into account the effects that wetland restoration might have on mosquito populations, nuisance-biting levels, and public and veterinary health. It is also necessary that such biodiversity initiatives have the knowledge and tools to enable them to assess and manage this impact as their work proceeds. It is crucial that environmentally-friendly mitigation strategies and wetland site locations are chosen with mosquito life histories in mind in order to minimise or avoid potentially deleterious effects. The environment sector recognises that there is a need for an evidence-base to inform future wetland creation and management initiatives. Applied correctly and, where possible, exploiting biodiversity and wetland management, they could become key tools in keeping mosquito populations at desirable levels.

Such strategies have been used to great effect in the United States (US) and Australia. The slogan 'Healthy Wetlands Devour Mosquitoes' is used by a number of US state authorities (IDNR, 2010). In Australia, the Wetland Link project promotes environmentally sensitive control of mosquitoes in wetlands by advocating a range of strategies related to changing depth of water, re-grading banks and culverts, introducing flooding and draining regimes, controlling floating and marginal vegetation and providing habitats and refuges for fish, invertebrate, avian and mammalian (i.e. bats) mosquito predators and competitors. Biorational agents such as *Bacillus thuringiensis* var. *israelensis* and the growth retardant Methoprene (Wetland Link, 2010) are also employed. In salt-marsh habitats 'Open Marsh Water Management' (OMWM) and 'runnelling' are now widely practised to control salt-marsh mosquito species (Russell, 2010). Great emphasis is given to a 'case-by-case' approach. However, in the UK and continental Europe there is little or no guidance for wetland managers on mitigation of a mosquito problem in an 'environmentally' sensitive way through wetland and vegetation management.

This article aims to firstly review briefly the wetland management and design strategies that have been employed to mitigate nuisance and disease transmission problems posed by mosquitoes in North America and Australia, and secondly to discuss the possibilities for similar mitigation in

Britain using similar methods, and focussing on the main wetland-associated nuisance and potential vector species identified by recent studies on British mosquitoes.

Wetland management strategies for mosquito control

Studies dealing with wetland management for mosquito control in Australia and North America (Sarneckis, 2002) conclude that, in general, wetlands with open water bodies, steep edges and little emergent vegetation tend to have diverse macro-invertebrate communities and low mosquito numbers. In contrast, wetlands with shallow water, sheltered, isolated pools limiting predator access and promoting poor water quality tend to have low macro-invertebrate communities and high mosquito numbers. In reality the distinctions between these two generic wetland types are not so distinct. Therefore it is worth reviewing some of the options that have been employed outside the UK and which may be applied to mitigate nuisance or vector activity by British mosquito species, bearing in mind the need for strategies to be developed on a case by case basis.

Predators

In the US, it is widely recognised that wetland restoration projects focusing on providing habitats for predators and competitors can have significant impacts on mosquitoes; for example one such study in Massachusetts reported a 90% reduction in mosquito numbers (USDA, 2008). This is largely explained by the fact that a restored wetland can reduce the incidence of flooding in areas that are not normally wet, and thus avoid the creation of aquatic habitats supporting mosquitoes but not their predators.

The role of, and provisioning for, invertebrate and vertebrate predators and competitors in limiting mosquito populations, particularly in healthy ecosystems, should be a main consideration when exploring options for controlling mosquitoes as part of an integrated environmentally friendly mosquito management system (Medlock & Snow, 2008a). In a British context, Medlock & Snow (2008b) reviewed the range of predators of British mosquitoes and a brief summary is provided here. This review incorporated several UK studies by Jefferies (1988), Lockwood (1986), Molenkamp (1998), Onyeka (1983), Onyeka & Boreham (1987), Roberts (1995), Service (1968; 1973a; 1973b; 1977), Service & Streett (1976) and Sulaiman & Service (1983), and previously unpublished work by the authors.

The main predators of mosquito larvae in permanent freshwater sites in the UK are anisopteran and zygopteran (Odonata) nymphs, adult and larval, dytiscid and halipid Coleoptera (in particular *Agabus bipustulatus, Dytiscus marginalis*, *Colymbetes fuscus* and *Hydroporus* sp.). Various hemipterans in the families Gerridae (e.g. *Gerris gibbifer/lacustris*), Notonectidae (e.g. *Notonecta glauca*), Hydrometridae (e.g. *Hydrometra stagnorum*), Corixidae (e.g. *Corixa punctata*), Nepidae (e.g. *Nepa cinerea*), and Veliidae (e.g. *Velia caprai*) are also reported as predators, as are various species of fish (e.g. *Phoxinus phoxinus, Alburnus alburnus*) and amphibians (e.g. *Rana temporaria, Bufo bufo, Trituris* sp.). Evidence of predation by these species has been reported on *Culex pipiens, Cx. torrentium, Anopheles claviger, Ochlerotatus punctor* and *Oc. cantans*.

In brackish salt-marsh habitats the principal predators are the brackish-water amphipod, *Gammarus duebeni* and the prawn/ditch shrimp, *Palaemonetes varians*. Specific studies have focussed on the impact of these species on *Ochlerotatus detritus*. The range of predators of mosquito larvae in containers is limited and largely dependent upon the permanence of the aquatic habitat and whether predator species have been able to colonise it. Predatory beetles are effective predators in such container habitats, as are fish, if they are permitted or able to colonise. Tree-hole mosquitoes similarly have very few, if any, predators of the larval stages, although there are several competitors (such as tree-hole midges, anthomyiid larvae, syrphid larvae and certain other Ceratopogonidae). However various arachnids associated with tree-holes (e.g. *Meta segmentata, Meta mengai*) have been reported to prey on emerging or ovipositing adult mosquitoes.

The most significant predators of emerging mosquitoes (i.e. adults emerging through the surface tension from the pupal casts) are predacious Diptera, primarily the Empididae (dance flies), Dolichopodidae (thick-headed flies) and to a lesser extent the Scatophagidae (dung flies) and Anthomyiidae. Particular species of note in relation to *Oc. cantans* from woodland pools are *Hilara interstincta, Hilara lugubris, Hilara pilosa, Rhamphomyia crassirostris* and to a lesser degree *Hercostomus* sp., *Campsicnemus survipes*, *Hydrophoria ruralis* and *Scatophaga squalida*. Odonata may also take mosquitoes as they emerge from aquatic habitats.

Following emergence, adult mosquitoes initially rest in vegetation where they are susceptible to a range of terrestrial invertebrate predators, and various species of arachnid have been reported to prey on mosquitoes during this stage. These include members of the following families: Argiopodae (orb-spiders, e.g. *Meta segmentata*), Linyphyidae (money spiders, e.g. *Linyphia* *peltata*), Thomiscidae (crab spiders, e.g. *Xytiscus lanio*), Lycosidae (wolf spiders, e.g. *Lycosa amentata*), Theridiidae (comb-footed spiders, e.g. *Theridion* sp.), Tetragnathidae (long-jawed orb weaver spiders, e.g. *Tetragnatha* sp.). Once airborne a wide range of species prey on adult mosquitoes including Odonata, a range of insectivorous birds and bats. For those species that undergo hibernation as adult female mosquitoes, various arachnids and possibly fungi are important in reducing the overwintering population.

Water and vegetation management

This paper aims largely to explore the potential for wetland management (water and vegetation) in the control of mosquito numbers, and there are various factors to consider that have been employed elsewhere. It is often a misconception that draining a wetland will reduce mosquitoes and remove the problem, Both naturally and artificially drained permanent wetlands can exacerbate the problem. There are three generic types of wetlands (Chase & Knight, 2003):

a) permanent wetlands that never dry, whereby the predators limit mosquito abundance,

b) temporary wetlands that dry yearly which have specialist predators and competitors that are well adapted to predictable drying and hence limit mosquito abundance through either lowering the rates of emergence (as a result of competitor density), and/or by increasing larval mortality, or by avoidance of oviposition by females in wetlands where competitor/predator numbers are high.

c) semi-permanent wetlands are wetlands that only dry during drought periods (i.e. when precipitation and the water table are particularly low). In such habitats the mosquito predators and competitors are eliminated, they are normally associated with permanent waters and cannot survive drying and must re-colonise following a drought. As a result the abundance of wetland mosquitoes can increase dramatically as mosquitoes have rapid generation times relative to their predators and can quickly disperse between habitats. Mosquitoes therefore show rapid population increases in semi-permanent wetlands in years following a drought event, prior to the build-up of invertebrate predator communities.

Additionally there are container habitats that periodically fill with water and are exploited by mosquitoes but rarely by their predators and competitors. Such habitats are often associated with urban areas and have facilitated the rapid establishment and global spread of invasive species, such as *Stegomyia albopicta* (also known as *Aedes albopictus*) and *St. aegypti* (also known as *Ae. aegypti*), and the consequent transmission of dengue and chikungunya viruses (Schaffner *et al*., 2009).

In the case of permanent or temporary wetlands some studies have shown that managing water levels to prevent draining can impact on mosquito larvae. For example maintaining high water levels in early spring, followed by drawdown (i.e. allowing water to recede to expose bare soil/vegetation) in late spring, can reduce mosquito populations as this can desiccate the larvae (Malan *et al*., 2009). After drawdown the water is allowed to return to pre-drawdown levels, however care must be taken in how this process of drying and flooding might adversely affect the aquatic flora and fauna.

Increasing the rate of water flow and aeration of the wetland can also impact negatively on mosquito larvae. Water flow, which may be subsurface flow, wind-assisted water movement or human-assisted turbulence (i.e. pumping), impacts the larvae by inhibiting their ability to acquire oxygen at the water surface (Dale & Knight, 2008; Malan *et al*., 2009). In ornamental ponds, the introduction of a waterfall or fountain is known to make the site inimical (USDA, 2008). Poor quality water, or water with high nutrient loading and sedimentation (e.g. by cattle/livestock entering the wetland) on the other hand can increase numbers of mosquitoes that prefer organic-rich waters (USDA, 2008). A study in California at a man-made wetland that received effluent containing high levels of ammonium nitrogen, used emergent vegetation as part of their water treatment process and found that at nitrogen levels above 6kg/ha/day, the abundance of mosquitoes increased ten-fold (Walton, 2001).

Deep water is generally considered unfavourable for mosquito larvae, and more favourable for their predators, such as fish. Design of meandering channel connections between shallow and deeper waters will allow a flow of predators into and out of habitats and therefore reduce mosquito numbers (USDA, 2008; Teels, 2009; Russell, 2009a). However, if wetlands are routinely drained, then internal re-grading (i.e. regular re-digging of a wetland to affect slope and depth and to remove silt build-up) will promote rapid dewatering (i.e. increased out-flow of water) and prevent pooling (i.e. smaller body of standing water) which will reduce mosquito colonisation (Russell, 2009a).

Controlling vegetation in wetlands is generally advised for controlling mosquitoes. This may be applicable for constructed wetlands, particularly those utilised in water treatment, but for biodiversity-rich wetlands, the removal of vegetation is perhaps not always desired, and would need to be considered on a case-by-case basis. Some suggest that periodic harvesting of dense stands of emergent vegetation will reduce mosquitoes and sediment build-up (Sarneckis, 2002). A wetland habitat with a simple shape, low edge-area ratio, steep banks and deep water has less vegetation and consequently fewer mosquitoes as emergent and floating vegetation provides shelter from the wind and predators and also promotes pooling (Sarneckis, 2002; Malan *et al*., 2009). Indeed, inundation of dried, dead emergent vegetation is known to greatly enhance mosquito production.

The dispersal of mosquitoes from wetlands to neighbouring towns and villages is often a concern but there is generally little known about dispersal ranges. Wetlands, if created, should ideally be located away from human populations, and beyond the flight range of important local mosquito species. However in areas of 'green living' where wetlands are created as part of ecological mitigation associated with a housing development, this might be difficult to achieve. In general most mosquitoes typically find bloodmeal hosts by following odour cues upwind, but disperse downwind, and this has been a consideration in locating new wetlands.

Salt-marsh specific issues

Aspects that exacerbate the potential nuisance caused by salt-marsh mosquitoes are related to a) the high marsh where pools of water in mud flats or salt-marsh vegetation are left by the highest tides, or alternatively are filled by rainfall/runoff or not flushed by daily tide movements, and b) the low marsh that is not well drained and where mosquitoes exploit impounded stagnant pools that are retained, usually due to siltation/blockage of tidal channels and hence not flushed. Management strategies include i) elimination of the potential aquatic habitat (by draining or filling), ii) modification (with water management), and iii) treatment with a control agent to kill the mosquito larvae. Elimination is usually not possible and treatment (more generally) is discussed below. Modification with 'Open Marsh Water Management' (OMWM) or the use of shallow ditches (runnels) has been reported to be acceptable, practical and effective (Russell, 2009b).

OMWM was developed to control mosquitoes by introducing their natural predators to areas of salt-marsh. With a system of pools connected by radial ditches, fish feed on mosquitoes during high tide, then retreat to sumps or reservoirs at low tide. OMWM has been found to be an effective long term method of controlling mosquito populations in salt-marshes without using sprays (Scheirer, 2009). OMWM promotes/restores 'full tidal flushing' by advocating the renovation of tidal channels and maintaining them in a condition which allows a) full tidal exchange and precludes the formation of impounded pools and b) 'natural dewatering' whereby salt-marsh pools that hold water after highest tides and rainfall are connected for tidal influence using various sized channels and with persisting ponds to support predatory fish (Russell, 2009b).

Runnelling is the creation of shallow, spoon shaped drains or 'runnels' that enhance tidal flushing of ponds isolated from main tributaries. Runnels may also provide access to mosquito habitats for fish that prey on mosquito larvae. Specifications for runnels are a) they should be hand-dug or constructed with minimal impact, b) be less than 30cm deep, with width:depth ratio of 3:1, c) should follow and be confluent with existing drainage lines, d) spoil created should be used as fill for very deep depressions or isolated pools, e) spoil should not to be used as levees, f) but can be broadcast if dispersed to undetectable levels (Anon, 2008).

Biological control of mosquitoes using larvicidal agents

A review of strategies would not be complete without mention of control using larvicides and three are generally used in larval mosquito control in wetlands in North America and Australia (Russell, 2009b). *Bacillus thuringiensis* var *israelensis* (Bti) is applied in liquid or solid formulations and lasts for 2/3 days. It needs to be ingested by larvae and acts by destroying the mid-gut. It must be applied within the first few days of the aquatic life of the mosquito as it is not effective against the later larval instars or pupae. It also has limited effectiveness in polluted water. Methoprene is applied in liquid and sand formulations, slow release granules or pellets. It acts upon the larvae as a growth regular, whereby the larvae survive but do not pupate. It is not effective in saline conditions. Finally, the organophosphate temephos is also used in freshwater habitats but it has detrimental effects on the development of some crustaceans in saline habitats.

Consideration of the British fauna

Possible options for wetland creation and management to mitigate biting by British mosquitoes, with specific reference to freshwater habitats, and how these might be utilised and incorporated into projects such as the Great Fen project (GFP) in Cambridgeshire will now be considered. For reference the GFP aims to connect two National Nature Reserves, Woodwalton Fen and Holme Fen, by transforming large areas of presently arable farmland into a landscape of wetland habitats over an area of 3700 hectares (Bowley, 2007). This land is initially being farmed pastorally, with the hydrological regime altered to allow for the development of wet grassland and fen, which will include seasonal and permanent open water. Over the long-term and in specific areas a more dynamic mosaic of reed-beds, wet meadows, scrub, wet woodland, and seasonal open water will be created. This project is a major flagship wetland creation initiative. The ultimate goal of the project is to serve the local community and region through providing increased opportunities for countryside recreation, contributing dramatically to the richness of local biodiversity, and improving the local quality of life. It is indicative of the many schemes that will follow through the Wetland Vision, an initiative that is backed by the UK Environment Agency, Natural England, the Wildlife Trusts and the UK Department of Environment. A recent report related to the mosquitoes of the Great Fen (Medlock & Vaux, 2009b) and the possible implications of wetland expansion on them highlighted the existence of twelve/thirteen mosquito species in a variety of different habitats and this section will focus primarily on these species:

1.	Reed-beds	*Aedes cinereus / Aedes geminus*
2.	Wet woodland	*Ochlerotatus cantans, Oc. annulipes, Oc. punctor, Oc. rusticus*
3.	Containers, tyre-tracks	*Culex pipiens* (nominate biotype), *Cx. torrentium*
4.	Vegetated ditches (fen)	*Coquillettidia richiardii, Anopheles claviger, Oc. caspius*
5.	Open un-shaded ditches	*Anopheles maculipennis* s.l.
6.	Non-specific ditches/ponds	*Culiseta annulata, Cs. morsitans*

Details of the distribution, biology, habitats, seasonality, host preference, nuisance value and vector status of these species are given in Tables 1, 2 and 3 and are not discussed further here. There follows discussion on possible mitigation strategies/issues and future field-based research requirements.

***Anopheles claviger* Meigen**

Anopheles claviger breed in ditches with dense vegetation, and is one of the commonest fenland and most widespread mosquito species in Britain (Snow *et al*., 1998; Hutchinson *et al*., 2007).

Overwintering is as larval instars II-IV in arrested development (Service 1968; 1973a). This species requires cold water, and is common in permanently wet habitats where they seek out shaded areas in pools, ditches and ponds, particularly those with floating (e.g. *Lemna*) and marginal vegetation (Snow & Medlock, 2008) or overhanging trees. The females seek cold water on which to oviposit and immatures actively avoid warming, and are only exceptionally found at temperatures as high as 20^{o}C (Coluzzi *et al*., 1965). Removal and cutting of vegetation in ditches has been shown to negatively affect larvae, with numbers only returning once the vegetation re-grows (Lewis, 1932). The requirements for perennial water-bodies and sheltered aquatic habitats (i.e. not in direct sunlight) suggest that either complete drainage of the aquatic site or removal of vegetation from ditches/ponds would significantly reduce the survival of the immature stages. Although complete drainage of the habitat would eradicate the larvae, it would also eradicate many of their predators and competitors (and potentially negatively impact biodiversity) thus later providing a predator-free aquatic habitat for opportunistic mosquito species to colonise. This approach is therefore not advised. If sufficiently healthy, permanent aquatic habitats, such as ditches, should have good populations of macro-invertebrate predators, and therefore managing these habitats to promote such predators (see above) is perhaps a more appropriate mitigation strategy for this species. Cutting vegetation to increase exposure to sunlight (and possibly predators), in order to reduce numbers of *An. claviger* larvae, could inadvertently provide a suitable habitat for the sun-loving open water *An. maculipennis s.l.*, so timing of cutting would need to be considered carefully. Further field studies that look at the role of brinking (cutting of marginal vegetation) and slubbing (de-silting of ditches) of ditches on the survival and re-colonisation of *An. claviger* are required. Owing to its ubiquity in Britain in vegetated ditches and ponds/lakes with dense marginal vegetation, *An. claviger* is likely to benefit from wetland expansion and expand readily to new wetland sites, albeit those adjoining existing habitats. However, further studies on their dispersal ranges are required. Although this species is widespread in the UK it is not currently associated with significant nuisance biting. Studies that continue to assess their human biting potential and their pest nuisance in neighbouring dwellings are nevertheless required, particularly given its ubiquity and predilection for ditches and ponds.

Anopheles maculipennis **Meigen sensu lato.**

The Palearctic Anopheles Maculipennis Complex comprises at least 10 species, almost all morphologically inseparable except in the egg stage (Linton *et al*., 2005), but only three, *Anopheles atroparvus, An. messeae* and *An. daciae* are known to occur in Britain: Studies of endemic malaria revealed the presence of the first two species early in the twentieth century, but *Anopheles daciae* was only recently identified through DNA analysis (Linton *et al*., 2005). Knowledge of its distribution, biology and ecology is therefore limited. The aquatic stages of *An. messeae* and *An. atroparvus* prefer relatively clean, permanent, standing or slowly moving water supporting algal growth or emergent vegetation, such as ditches, drains, slow moving rivers, ponds and marshes. Larval stages of these species may occur together, although *An. atroparvus* tolerates higher saline concentrations and has a more coastal and estuarine distribution. Both species overwinter as a generation of nulliparous, inseminated females exhibiting ovarian diapause. *Anopheles meseae* invariably chooses cold overwintering sites in which it remains in deep hibernation until reactivation in the spring. Some specimens of *An. atroparvus* overwinter in the same cold sites. However, most remain in buildings in which the summer generations fed and rested, and take occasional winter bloodmeals on the vertebrate occupants, which merely serve to replenish or maintain fat reserves which are depleted more rapidly in warmer situations (Ramsdale & Wilkes, 1985).

Anopheles maculipennis s.l. favours sunlit permanent waters, and it is possible that when well maintained open sunlit ditches designed for farmland use become more overgrown and incorporated into fen systems, their suitability for *An. maculipennis* s.l. declines; thus becoming increasingly suitable for *An. claviger,* which itself can tolerate a wide range of pollutants but demands cold water. Hutchinson *et al*. (2007) reported only 5% of the anophelines caught at Wicken Fen were *An. maculipennis* s.l., and it would be useful to investigate the changing proportions of these species compared to *An. claviger* as ditches become incorporated into vegetated fen habitat. The effect of degrees of shade and vegetation on mosquito species diversity and abundance in freshwater wetlands requires further study, as does the impact of brinking and slubbing on the relative proportions of the different species. For example, a process of brinking (cutting vegetation) to create sunlit water, and slubbing, to remove sediment, will create a cycle within ditches that initially are suitable for *An. maculipennis* s.l., but over time becomes more vegetated, thus favouring *An. claviger* until they are managed again. However, the effect on water temperature will be crucial.

Similarly the identification of key hibernation sites may provide an opportunity for reducing the overwintering population of *An. maculipennis* s.l.. It is likely that wetland expansion will increase the number of aquatic habitats suitable for *An. maculipennis* s.l. and given its association with malaria, a greater understanding of favoured ecological niches is required.

***Coquillettidia richiardii* (Ficalbi)**

Coquillettidia richiardii is particularly common in fen, ditch and pond habitats and its preference is explained by its specific life-history and behaviour. It is unique among the British fauna in that it can extract oxygen from plants; their larval respiratory siphon and pupal trumpets are specialised for piercing aerated stems and roots of aquatic plants (e.g. *Acorus* [sweet flag], *Glyceria* [grasses], *Ranunculus* [water crowfoot], *Typha* [reedmace] (there are no records in Britain associated with *Phragmites* [common reed])). This ability negates the need for the immature stages to come to the surface to obtain oxygen. Although occasionally the earlier instars will respire at the water surface, the older larvae and pupae have an obligatory need for plants (Marshall, 1938). *Coquillettidia richiardii* overwinter as 4^{th} instar larvae, able to survive under ice, with adults appearing only from June-September, most numerously in July-August (Marshall, 1938; Service, 1968; Snow & Medlock, 2008), when they can be a nuisance to humans, with records of them entering houses to feed (Service 1971). There is very little information on dispersal ranges or mitigation strategies of this specialised species. Owing to their larvae having an obligatory need for aquatic plants, the possible impacts of cutting appropriate vegetation could be explored. Although not currently field tested it may be that vegetation cut to below the water level (or indeed flooded) during winter might inhibit respiration by overwintering 4^{th}-instar larvae, however, this requires further research. Complete drainage of the aquatic habitat would negatively impact this species, and the implications of draining permanent healthy ditch ecosystems have already been discussed. The creation of new vegetated ditch/fen habitat and ponds (inc. garden ponds) with particular marginal vegetation will favour the colonisation of this species. The larvae are notoriously difficult to find, and the roots and stems of plants have to be physically removed and inspected. This makes locating particular aquatic sites difficult. The preference for particular plants species should act as a guide for the most likely sites for larval development, but confirmation will be hampered by the difficulties in surveying larvae. Nevertheless, the collection of adults in various forms of adult trap should provide sufficient evidence of their colonisation. Further research on this species should focus on assessing their dispersal ranges and the impact of cutting vegetation on immature survival.

***Aedes cinereus* Meigen / *Aedes geminus* Peus**

Aedes cinereus and *Aedes geminus* are morphologically similar, occurring in temporary freshwater habitats such as flooded grasslands, reed-beds and the flooded margins of permanent ponds. The occurrence of *Ae. geminus* in the UK has only recently been confirmed (Medlock & Vaux, 2009a) and little is known about its biology/ecology, although it is assumed to be similar to *Aedes cinereus*, perhaps occurring together. *Aedes cinereus* appear to remain in the egg stage for sixth months of the year, with eggs laid in low-lying situations that habitually flood during rainy periods (Marshall, 1938). Service (1968; 1971) showed that the majority of eggs require 8-12 soakings before they will hatch which might explain the apparent late hatching of eggs from April onwards. The mitigation options for these two species could therefore be to exploit the flooding/draining regime of reed-beds and allied habitats (i.e. flooded grasslands) so as to impact on the life history of this species. It should be noted that given this species can withstand long periods as non-desiccating eggs it should not be assumed that eggs will not survive through to subsequent years for later emergence. However there is evidence that some eggs require at least eight soakings before they will hatch and therefore a structured flooding/draining regime could be devised if this species was considered a nuisance or disease vector. There is no information on the natural predators of this species (Medlock & Snow, 2008b), and although it might be argued that owing to the transient nature of its aquatic site the role of competitors and predators is lessened, this is not the case in transient aquatic habitats in wet woodland. At Woodwalton Fen, this mosquito was a significant biting nuisance in reed-beds, with little activity on neighbouring paths (Medlock & Vaux, 2009b), suggesting that dispersal of this species may be restricted. However, given that the first stage in returning arable land back to wetland involves the creation of flooded grassland (i.e. by raising the water level in post-arable land), the opportunities for this species to colonise as a pioneer species of new wetlands need to be considered. Further information and research is required on egg longevity, adult dispersal rates and the impact of premature drying of reed-beds/grasslands on larval development and survival. *Aedes cinereus* has also been reported to bite birds and to be an important bridge vector of Sindbis virus in Sweden (Medlock *et al*., 2007) and feed also on cattle in England (Service, 1969; 1971). The occurrence of cattle grazing in reed-beds/flooded grasslands during the summer months could provide an important blood source for *Ae. cinereus,* and divert biting activity away from humans. Given the association of *Ae. cinereus* with mosquito-borne bird viruses it would be interesting to study the proportion of engorged females having fed on birds compared to cattle. Further information on the distribution and abundance of *Ae. geminus* in the UK is required. Differentiation between these two species is explained by Medlock & Vaux (2009a), suffice to say that surveys should focus on sweep netting male mosquitoes or rearing larvae through to male imagos to enable inspection of the relative sizes of the internal (larger in c*inereus*) and external (larger in *geminus*) ramifications of the male gonostylus.

Ochlerotatus cantans **(Meigen) and** ***Ochlerotatus annulipes*** **(Meigen)**

Owing to their habit of laying eggs in dried-up hollows in woodland subject to periodic flooding, the immature stages of *Ochlerotatus cantans* and *Ochlerotatus annulipes* are typically found in shaded woodland pools and wet woodland, and are often found breeding together in the same aquatic site (Snow & Medlock, 2008). Both species are aggressive human biters. These two species are morphologically similar and distinguishing features are described by Snow (1990) and Schaffner *et al*. (2001). They are univoltine species (Service, 1968), with eggs laid in damp leaf litter of shaded pools which was deposited during dried out periods, usually in June-September. Eggs do not hatch when flooded by autumn rains as they require environmental conditioning brought on by cold temperatures, with the majority of eggs hatching incrementally up to late-March (Service, 1977), by which time the densely shaded pools are heavily infested with larvae which continue to appear over the next four months. Mitigation from the attentions of this mosquito could be effected by identifying aquatic sites by larval sampling and draining them, however this is only practical if the hydrology is permissible. Alternatively where sites are annually transient there are usually a good number of predators and competitors adapted to that habitat. Studies by Service (1973b; 1977) found that during the season dance-flies accounted for the loss of 13% of the emerging imagos. Although not enough to eliminate the species, when coupled with other predatory invertebrates, dance-flies could have a notable impact on emerging adults. There is a suggestion that removing vegetation around a pool leads to the eradication of *Oc. cantans* larvae (Marshall, 1938), however this requires further research. Undoubtedly creation of wet woodland will lead to colonisation by these woodland *Ochlerotatus* species. The vernal activity of the immature stages in isolated pools provides an opportunity to render populations unviable through targeted draining or, where possible, the introduction of key predator species. However this is only likely to be applicable in heavily managed and confined landscapes and the possibilities for control rather depend on the nature of the aquatic habitats and hydrology. Alternatively, perhaps making smaller habitats more permanent (thus avoiding summer drying), with steep sides, may lessen the impact of seasonal flooding, thus making such sites less attractive to ovipositing females of these species. Managing water levels in large ranging swamp habitats could prove difficult. In Woodwalton Fen these species were found associated with large and small ditches and depressions prone to seasonal flooding (Medlock & Vaux, 2009b). In other sites, such as in Epping Forest, they have exploited huge borrow pits, a legacy of the levees created for the forest roads (Snow & Medlock, 2008). Creation of new wet woodland should consider the proximity of neighbouring dwellings as these species are likely to become a nuisance. Owing to their catholic feeding habits, their possible involvement in virus transmission cycles ought also to be a consideration. Further studies are required on the impact of removing scrub surrounding aquatic sites on immature survival, the dispersal ranges of blood-seeking females, and further studies on the interactions and co-existence of the two species.

***Ochlerotatus punctor* (Kirby) and *Ochlerotatus rusticus* (Rossi)**

Ochlerotatus punctor and *Oc. rusticus* occupy niches similar to those of *Oc. cantans* or *Oc. annulipes,* all are mosquitoes of temporary woodland pools. Marshall (1938) reported that immatures of *Oc. punctor* are often found in more or less acid waters in sandy and gravelly pools lined with dead leaves or *Sphagnum,* or in open heath or woodland where birch or pine predominate. It is possible that this species is associated with acid heath habitats. *Ochlerotatus rusticus* appears to prefer pools bordered by deciduous hedges and trees, often lined with dead leaves upon which the larvae feed (Cranston *et al*., 1987). Further work is required to understand whether specific niches exist for each woodland *Ochlerotatus* species, which possibly require different degrees of shade, amount of leaf litter and acidity of the larval habitat. It is likely that these species will benefit from the creation of woodland pools, albeit perhaps on acid soils, which suit *Oc. punctor* at least. As with *Oc. cantans*, the impact of changing hydrology during winter/early spring and the maintenance of these aquatic sites through to April are likely to be important factors in determining the temporal survival of immature populations.

***Culex pipiens* Linnaeus. and *Culex torrentium* Martini**

The Subgenus *Culex* is represented in Britain by *Culex (Culex) pipiens* Linnaeus and the morphologically similar *Cx. (Cux.) torrentium* Martini*,* with wide sympatric distributions in Britain and elsewhere in Europe. However, the taxon *Culex pipiens* comprise two subspecies, the Holarctic *Cx. pipiens* Linnaeus sensu stricto, which additionally occurs in southern Africa and South America, and the subpecies *Cx. pipiens pallens* Coquillett with a Far Eastern distribution, but which is also present in Mexico and parts of the USA (Harbach, 2011).

Both *Cx. (Cux) pipiens* and *Cx. (Cux) torrentium* are currently classified in the Pipiens Group of the subgenus, with the Holarctic *Cx. pipiens* placed in the Pipiens Subgroup, and the Palaearctic *Cx. torrentium* placed in the Trifilatus Subgroup, which additionally contains New Zealand, Pacific Islands, Chinese, Indian and southern African species (Harbach, 2011). *Culex pipiens* and *Cx. torrentium* are morphologically similar and reliable diagnostic characters are confined to adult male genitalia (Cranston *et al*., 1987). However, the situation is complicated by the presence of two biotypes of *Cx. pipiens* Linnaeus. The nominate *pipiens* biotype, like *Cx. torrentium,* is anautogenous, strongly ornithophilic, and develops in a wide variety of rural, suburban and urban natural and artificial water collections such as ponds, ditches, tanks and butts, in which they are often found together. Both overwinter in complete hibernation in cold out-buildings, cellars or natural shelters (Cranston *et al*., 1987; Snow, 1990). In contrast, the *molestus* biotype of *Cx. pipiens* is autogenous, exhibits catholic host preferences and, in northern Europe, both developmental and adult stages are confined to hypogeal (usually urban) situations offering shelter from adverse winter conditions where, if hosts are available, as in deep mines, subterranean transport systems such as the London Underground or tenement blocks (Snow, 1990), it can be a troublesome pest throughout the year. Autogeny is a last resort enabling persistence through adverse periods even in the absence of hosts. This biotype exhibits a wide tolerance of water pollution, from clean water in containers to highly polluted water in sewage storage and treatment plants (Cranston *et al*., 1987, Snow, 1990). The marked ornithophilic preferences of *Cx. torrentium* and the nominate biotype of *Cx. pipiens* make both prime suspects of arbovirus transmission between birds, and the more catholic host preferences of the *molestus* biotype marks it as a vector between birds, a bridge vector and a vector between mammals, including humans.

The opportunistic nominate biotype of *Culex pipien*s is common in a variety of more or less transient aquatic habitats in wheel ruts and containers associated with wetland habitats. Mitigation in some, but not all, sites is easily achievable through controlling pooling caused by vehicles and by reducing the numbers of container habitats. This biotype is a typical pioneer and it is likely that during the first stage of wetland regeneration, it will exploit new wetland pools and flooded grasslands, as currently occurs in the Great Fen (Medlock & Vaux, 2009b), as well as container habitats associated with the declining farms. Further field work is required to establish the incidence of permanent water in ditches and flooded arable land colonised by this biotype and the ecologically similar *Cx. torrentium*, and the proportions of each taxon in different kinds of hibernation site. Identification of key hibernation sites (e.g. in bird hides) may provide an opportunity for reducing overwintering populations.

Culiseta annulata **(Schrank)**

Culiseta annulata is a widespread and abundant mosquito. Although often a biting nuisance in urban areas where it exploits container and organic-rich habitats (e.g. cisterns and water butts), it is equally found in a wide range of natural aquatic habitats such as ponds, ditches, and marshes in sunlit and shaded conditions; and in clean, fresh, polluted or brackish water (Snow, 1990), and it is also a troublesome rural pest. At Wicken Fen it was the fourth most common species (after *An. claviger, Cq. richiardii, Oc. annulipes*) representing 5% of the entire catch (Hutchinson *et al*., 2007). At Woodwalton Fen larvae of *Cs. annulata* were abundant in woodland pools during July and August, and this species may be a consideration in the creation of wet woodland. Information on the seasonality of human biting and their dispersal range will aid the assessment of the risks posed by this species, along with further studies into their specific aquatic sites in natural wetland habitats. This species will benefit from wetland expansion and present a biting nuisance. Owing to its impartial choice of avian and mammalian, including human, blood (Service, 1969), it may also be a key potential vector. *Culiseta annulata* appears to be able to survive winters without recourse to diapause, and aquatic stages, males and gonoactive (including parous) females may be found throughout the winter (Ramsdale & Wilkes, 1985). It also has the longest biting season of any British species and may be a biting nuisance throughout the year.

Culiseta **(*Culicella*)** ***morsitans*** **(Theobald)**

Culiseta morsitans is a common species in wetlands in Britain. Lewis (1932) considered it the most common mosquito of fenland habitats, where larvae abound in shallow water among the sedge, *Cladium mariscus*. The eggs are laid above the water level and hatch following immersion by autumn and winter rainfall, with the majority hatching on first flooding. However, the eggs are drought resistant and remain viable even when dried out for long periods during exceptionally dry winters (Service, 1994). This species feeds almost exclusively on birds (Service, 1969) and may be collected at roosting elevations, although some feeding on humans has been reported. This species is not likely to be a biting nuisance, but like *Cx. pipiens* its ornithophilic nature makes it a suitable enzootic vector of bird-associated viruses (Medlock *et al*., 2005; 2007). This species is not particularly attracted to light- or CO_2-baited traps in Britain (Service, 1994), and therefore may be under-represented in sampling methods employing these traps. It additionally exploits a number of shaded aquatic habitats in ditches, wet woodland, reed-beds and the margins of open water. In the absence of pathogen transmission and human biting, it is questionable how important this species is to human health, although its possible status as an enzootic vector should not be ignored. Care must be taken in separating this species from the other morphologically similar British species, *Cs.* (*Cuc.*) *litorea* and *Cs.* (*Cuc.*) *fumipennis* (Ramsdale & Snow, 1994; Schaffner *et al*., 2001; Medlock & Vaux, 2010).

Discussion of other British mosquitoes (including salt-marsh species)

Ochlerotatus caspius, Oc. detritus, Oc. dorsalis, Oc. flavescens and *Culiseta litorea* are brackish water mosquitoes, although *Oc. caspius* may also be found in fresh water habitats, including Wicken and Woodwalton Fens. Further research is required on the suitability of open marsh water management (OMWM) and runnelling for reducing the nuisance caused by these species. Furthermore, careful ecological consideration of the impact of these strategies on the conservation of flora and fauna must be addressed. The creation of new salt marsh will provide new habitats for *Oc. detritus*, a persistent nuisance in estuarine and coastal areas such as the Dee Estuary where long term mosquito control with larvicides is necessary. *Ochlerotatus detritus* and a sibling species *Oc. coluzzii* are sympatric in continental coastal situations. However, *Oc. detritus*, a notorious pest in the upper Rhineland, also has an extensive inland distribution in Europe. Inland records in Britain are rare, but occasionally occur, with collections from brackish water near Droitwich, Worcestershire (Marshall, 1948) and in the Crewe/Northwich area, Cheshire (Burke, 1946), from fresh water at Woodwalton Fen, Huntingdonshire (Service, 1972) and a *Typha/ Juncus* marsh amongst slag heaps with a probable high mineral sulphite content near Oulton, West Yorkshire (Service, 1973). Recent unpublished studies by the authors have found significant populations of *Oc. detritus* at Woodwalton Fen; presumably associated with freshwater. Further DNA studies are underway to confirm whether this is actually an inland population of *Oc. detritus* s.s. and whether distinctions exist between this population and coastal populations of *Oc. detritus* s.l. Through comparison of different UK populations through DNA analysis, it may be that coastal populations of *Oc. coluzzii* also occur in the UK.

A further two species are locally distributed, although abundant where they occur: *Culiseta alaskaensis* is a northern species, with records from North Yorkshire and Scotland, *Anopheles algeriensis* is a Mediterranean and Middle Eastern species with isolated northern European populations in Germany and Britain, where it is well established in parts of the Norfolk Broads and on Anglesey (Edwards, 1932; Rees & Rees, 1989; Snow, 1998).

Culiseta (*Cus.) subochrea* (morphologically and ecologically similar to *Cs.* (*Cus.) annulata*), *Culiseta* (*Cuc.*) *fumipennis,* and *Culex (Neoculex) europaeus* are less often encountered and should be considered further where they occur. Information on their biology and ecology in the UK is so sparse but they appear to have little or no vector or nuisance significance. A further three species, *Anopheles plumbeus, Dahliana geniculata* and *Orthopodomyia pulcripalpis* are tree-hole species and are therefore not likely to be impacted by wetland creation, expansion or management, although they may be associated with birds roosting in mature trees in or near wetland habitats.

A total of 34 species have been recorded in Britain and brief mention is made here of the remaining species. *Aedes vexans*, a floodwater species, has been recorded in 12 vice counties and viable populations are known from at least two sites in Essex (Snow & Medlock, 2008). Five species, *Culex* (*Barraudius*) *modestus* (recorded during 1940s in Portsmouth), *Culiseta* (*Allotheobaldia*) *longiareolata* (3 records: Hampshire, Dorset, Surrey), *Ochlerotatus leucomelas* (1 record: Nottinghamshire), *Oc. sticticus* (3 records: Cumbria, Hampshire, Perthshire) and *Oc. communis* (1 record: Nottinghamshire) are either rare or doubtfully native: (Medlock & Snow, 2008a). That is not to say that they do not or have never occurred in Britain and further surveys may provide new information on the status of these species. For example, recent unpublished field studies by the authors and colleagues have identified a possible established population of *Culex modestus* in the UK. Additionally, it may be that other European arbovirus vectors such as *Oc. sticticus* which is widespread in northern Europe, but seemingly rare in the UK, may still occur in restricted foci. However, wild specimens of many species are notoriously difficult to separate morphologically as Overgaard Nielsen *et al.,* (1995) who compared morphological and allozyme electrophoresis identifications on the same specimens in Denmark, convincingly showed. Uncertainty over the identity of rarely reported species demands employment of modern sophisticated discriminatory technology.

Conclusions and further research

This paper highlights a number of mosquito species that are likely to be impacted upon by wetland expansion. Focus is given to discussion on the possible mitigating strategies that could employ water and vegetation management to impact on the life cycle of these species in a variety of wetland habitats (e.g. fen, ditch, reed-bed, wet woodland, flooded grassland, ponds and pools) and consequently reduce mosquito numbers, without inadvertently affecting biodiversity. This article has highlighted a number of research questions that still need to be addressed before the impacts of wetland creation and expansion on British mosquitoes and mosquito-borne disease, now and in the future can be understood. A number of recommendations for follow up work in the UK are listed below, many of which are now being addressed through extensive field-based research in the Great Fen. Similar studies are also commencing in newly-created salt-marsh habitats relating to coastal re-alignment schemes (to assist with coastal flood alleviation) and compensatory coastal habitat schemes (to mitigate the loss of European protected coastal habitat sites through port expansion/development):

1. To investigate the types of wetland to be created and the significance of each as an aquatic habitat for the existing mosquito fauna.
2. Describe the seasonality and abundance of larval and adult populations within these habitats,
3. Describe how hydrological changes associated with the management of different wetland types might impact on the life-histories of the different mosquito species,
4. Understand the importance of habitat structure governing species diversity and distribution (including the impact of ditch brinking and slubbing),
5. Identify, based on 1- 4, habitat management strategies to mitigate nuisance species,
6. Conduct human landing catch studies to ascertain seasonality of activity and biting of nuisance species,
7. Conduct dispersal studies to ascertain the range of activity of nuisance species, and hence their impact on local dwellings and human populations,
8. Understand the temporal change in species diversity and abundance through the course of wetland creation (from arable to fen),
9. Conduct virological testing for the occurrence of pathogens,
10. Develop strategies to inform wetland creation and management plans to mitigate nuisance biting and potential pathogen transmission through designing, locating and managing new and existing wetlands on a case-by-case basis.

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Table 1: Most common British species by principal aquatic breeding site (adapted from Medlock & Snow, 2008a)

Temporary fresh water pools
(e.g. flooded meadows, woodland pools, ditches)

Ae. cinereus
Ae. vexans
Oc. (*Och.*) *annulipes*
Oc. cantans
Oc. (*Och.*) *flavescens* (also brackish habitats)

Oc. punctor
Oc. (*Rus.*) *rusticus*

Underground water
(e.g. water in basements, mines, underground train tunnels, broken drains and other cloistered water collections, e.g.)

Culex pipiens biotype *molestus*

Temporary saline water pools
(e.g. saltmarsh, areas subjected to tidal incursion)
An. atroparvus
Oc. caspius
Oc. (*Och.*) *detritus*
Oc. dorsalis

Permanent ground water
(e.g. ditches, pools, ponds, canal and river edges)
An. claviger
An. daciae
An. messeae
Coquillettidia richiardii
Cs (Cuc.) fumipennis
Cs. (Cuc.) litorea
Cs. (Cuc.) morsitans
Cx. (Ncx.) europaeus

Artificial water collections
(e.g. tanks, rain barrels, wells, cisterns, troughs, buckets, cans)
Cx (*Cux.*) *pipiens* nom. biotype
Cx (*Cux*). *torrentium*
Cs (Cus.)) annulata
Cs. (Cus.) subochrea

Tree holes
(e.g. rot holes and pans)
An. plumbeus
Dahliana geniculata
Orthopodomyia pulcripalpis

Ae. = Genus *Aedes; An.* = Genus *Anopheles; Cs.* = Genus *Culiseta; Cus.* = Subgenus *Culiseta; Cuc.* = Subgenus *Culicella; Cx.* = Genus *Culex; Cux.*= Subgenus *Culex; Ncx.* = Subgenus *Neoculex; Oc.* = Genus *Ochlerotatus;* Aedine species names not preceded by a three letter prefix have not yet been assigned to a Subgenus (Reinert, Harbach & Kitching, 2009).

Table 2. A summary of the seasonal activity of larvae and adults of key freshwater mosquito species likely to be affected by wetland expansion.

Seasonal activity larvae

Species	J	F	M	A	M	J	J	A	S	O	N	D
Aedes cinereus/geminus				I	II-III	II-P						
Anopheles maculipennis s.l.			EI	II-P	E-P	E-P	E-P	E-P	E-P			
Anopheles claviger	D	D	R	II-IV	P	EI	II-IV	II-P	II-P	I	II-IV	II-IV
Coquillettidia richiardii	II-IV	II-IV	II-IV	II-IV	II-P	I-P	I-P	I-4	I-4	II-IV	II-IV	II-IV
Culex pipiens nominte biotype				E-III	II-P	II-P	E-P	E-P				
Culiseta annulata	E-P	E-P	E-P	E-P	E-P	E-P	E-P	E-P	E-P	E-P	E-P	E-P
Culiseta morsitans	E-IV	E-IV	E-IV	P	P	P				E	E-IV	E-IV
Ochlerotatus annulipes	E-III	E-IV	I-P	I-P		E	E	E	E	E	E-II	E-II
Ochlerotatus cantans	E-III	E-IV	I-P	I-P		E	E	E	E	E	E-II	E-II

Seasonal activity adults

Species	J	F	M	A	M	J	J	A	S	O	N	D
Aedes cinereus/geminus							A					
Anopheles maculipennis s.l.						A	A					
Anopheles claviger					A	A		A	A			
Coquillettidia richiardii							A	A				
Culex pipiens nominte biotype	D	D	D			A	A		D	D	D	D
Culiseta annulata												
Culiseta morsitans						A						
Ochlerotatus annulipes							A					
Ochlerotatus cantans							A					

From: Marshall 1938; Service 1968; 1969; 1971; 1973a; 1977; 1994; Snow and Medlock 2008; Snow 1990; Cranston *et al*. 1987

D	Diapause state
R	Reactivation
E	re-appearance of eggs
I	1st instar
II	2nd instar
III	3rd instar
IV	4th instar
P	pupae
A	Adult peak

Table 3. A summary of biological, behavioural and disease parameters relevant to the key freshwater species likely to be impacted upon by wetland expansion.

Species	**Aquatic habitat**	**Relative abundance in fenland habitat: Wicken Fen (WKF)[1] Woodwalton Fen (WWF)[2]**	**Overwintering stage & voltinism[3]**	**Biting preference[4]**	**Nuisance status Potential vector status[5]**
Anopheles claviger	Shaded pools, ditches and ponds, particularly those with floating or marginal vegetation, or the margins of ditches sheltered under trees	most commonly trapped species at WKF (1174/2655: 44%) and second most common at WWF	Larvae (instars II-IV) in arrested development. Bivoltine	Readily bites humans, also rabbit and bovid	Absence of bird biting records suggest limited vector of WNV or SINV. Not considered main malaria vector in UK historically.
Coquillettidia richiardii	Vegetated ditches, requires species for plants	Most common at WWF. Second most common at WKF in Mosquito Magnet (25% catch) and most common in the CO_2 CDC light trap (54%; 500/921).	Univoltine. Overwinter as larvae. 1st instars June-Sept; all other instars present all year.	Mainly on humans and other large mammals, but also birds, rabbits and amphibians.	Putative vector of WNV. Biting nuisance but limited to a peak in July/August.
Aedes cinereus / Aedes geminus	Reed-bed, flooded meadows, ponds, ditches, marshes.	Very abundant at WWF.	Univoltine. Remain in egg stage for 6 months; Eggs require up to 8-12 soakings.	Readily bites humans, cattle, and birds.	Putative vector of WNV. Bridge vector of SINV in Scandinavia, and potential vector of TAHV.
Ochlerotatus cantans / Ochlerotatus annulipes	Shaded woodland pools, with eggs laid in dried up hollows subject to flooding.	Large numbers (>600) of *Oc. annulipes*, low numbers (~10) of *Oc. cantans* at WKF. Both found in large numbers at WWF.	Univoltine. Eggs laid in damp leaf litter June-Sept; eggs require cold temperatures to stimulate hatching in spring.	*Oc. annulipes* bites humans and cattle. *Oc. cantans* bites cattle, rabbits, humans, birds, and horses.	*Oc. cantans* a potential vector for WNV, SINV, and TAHV.
Culex pipiens	*Cx. pipiens* biotype *pipiens* in natural and artificial water. At WWF wheel ruts,	WKF found higher number of *Cx. pipiens* s.l. in CO2 baited CDC light-traps than in Mosquito Magnet.	*Cx. pipiens* biotype *pipiens* - Multivoltine. Inseminated females hibernate, and lay	*Cx. pipiens* biotype *pipiens* bites birds. *Cx. pipiens* biotype *molestus* is	*Cx. pipiens* biotype *pipiens* is an important enzootic vector of bird-associated viruses (WNV, SINV). *Cx. pipiens*

	shallow standing water, and containers. *Cx. pipiens* biotype *molestus* usually in flooded underground chambers.	Found in good numbers at WWF.	eggs in spring following a blood-meal. *Cx. pipiens* biotype *m molestus* – does not hibernate	mammalophilic, but also feeds on birds.	biotype *molestus* is a potential bridge vector of WNV
Anopheles maculipennis s.l.	*An. messeae* prefers clean, permanent, standing water supporting algae. *An. atroparvus* similar habitat but can tolerate high salinities.	<65 / 1275 Anophelines were *An. maculipennis* s.l. at WKF. Low numbers of larvae in sunlit ditches in WWF.	Both species overwinter as nulliparous, inseminated females. *An. messeae* hibernates in cool shelters. *An. atroparvus* prefers warmer animal shelters and takes bloodmeals throughout winter.	Both species feed on animals, but not significantly on birds.	Historical vectors of malaria in Britain.
Culiseta annulata	Range of habitats including containers, ponds, ditches, marshes, in sunlight or shade.	4th most common species (191/3576) at WKF.	Multivoltine. Overwinters without diapause.	A broad range of hosts including humans, birds, rabbits, pigs and no doubt other mammals/livestock.	Aggressive human biter. Putative vector species - implicated as a potential bridge vector of WNV & TAHV.
Culiseta morsitans	Fresh or slightly brackish ponds, ditches, and pools – shaded or open.	9% of catch in CDC light traps in WKF. WWF – low numbers.	Univoltine. Eggs hatch following immersion by autumn or winter rainfall; eggs can survive desiccation; larvae can withstand freezing.	Feeds exclusively on birds.	Ornithophilic nature makes it suitable as an enzootic vector of bird-associated viruses (WNV, SINV).
Ochlerotatus punctor	Woodland pools, especially those lined with dead leaves.	WKF only one individual. Only one found at WWF.	Univoltine. Adults peak in June. 4th instar larvae found in December, but pupation deferred until April.	Aggressive biter of humans. Also cattle, and birds.	Putative bridge vector of WNV.

[1] – study conducted at Wicken Fen, Cambridgeshire: June – September, 2003 (Hutchinson *et al.*, 2007), and 1932 (Lewis, 1932)
[2] – study conducted at Woodwalton Fen, Cambridgeshire: August – September, 2009 (Medlock & Vaux, 2009)
[3] Marshall, 1938; Service, 1968; 1971; 1973a; 1994; Snow & Medlock, 2008
[4] Service, 1969; 1971; Cranston *et al*., 1987; Snow, 1990; Medlock *et al*., 2005
[5] This table only includes known European arborivuses: Medlock *et al.*, 2005; 2007; Snow, 1999; Service, 1971