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Mosquito diversity and abundance in English wetlands – empirical evidence to guide predictions for wetland suitability for mosquitoes (Diptera: Culicidae)

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Abstract

The absence of habitat-based guidance for wetland managers on the British mosquito assemblages has in recent years prevented development of the ecological aspect of medical entomology in the UK. This has been particularly relevant in the context of emerging mosquito-borne disease and the creation of wetlands for biodiversity and flood-alleviation goals. This study aimed to provide empirically derived habitat-based predictions in order to assess the suitability of English wetland habitats for mosquitoes. Entomological field data on mosquito density and diversity were collected at 12 English wetlands in 2017 and 2018 using immature and adult mosquito surveys. Wetlands were chosen representing a number of wetland categories that included coastal, urban, wet woodland and established freshwater wetlands to identify key species and functional groups to inform predictions of mosquitoes by aquatic habitat type. Nineteen species were recorded from eight functional groups, totalling 38,577 adult female (19 mosquito species groups) and ~2,000 immature mosquitoes in 13 aquatic habitat types. Approximately 90% of all trapped mosquitoes were attributed to one of five species groups. The most common species were: *Aedes* (*Och.*) *caspius* (Pallas, 1771) (~35% of all mosquitoes), associated with coastal estuarine and flooded grassland sites, *Ae. cantans/annulipes* (19.7%) in wet woodland field sites, *Anopheles claviger* (16.2%) and *Coquillettidia richiardii* (12.6%) with the widest occurrence, found in nearly all field sites, and *Ae. detritus* (6.9%) in brackish field sites. Across the study, adult mosquito activity increased from week 21 with wet woodland *Aedes* mosquitoes, until week 40 with open-flood water species, with greatest diversity of species during weeks 23–30. The resulting data inform efforts towards developing predictive tools for non-entomologists to accurately predict the presence and abundance of British mosquitoes in a given habitat, using local knowledge of seasonal aquatic habitats.

Keywords

ecology – *Aedes*, *Culex* – UK – management

1 Introduction

The global health emergency associated with the mosquito-borne Zika virus in 2015–2016 highlighted the potential for new and exotic mosquito-borne diseases to emerge rapidly and in new geographic areas, primarily in urban areas, as well as to cause millions of cases of a previously unknown clinical disease of concern (WHO, 2022). Zika however, was at the time the latest arthropod-borne virus to emerge in the Americas after

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a large regional outbreak of chikungunya virus in 2013, periodic outbreaks of dengue, as well as the introduction and subsequent large outbreak of West Nile virus in North America from 1999 (Hayes and Gubler, 2006). Although several of these infections are associated with non-wetland habitats, it has raised the profile of mosquito-borne arboviruses, and their potential emergence in the UK.

In Europe, outbreaks of West Nile virus have been reported every year over the last two decades, and although the numbers of human cases are not comparable with North America during the early years of their outbreak, there were over 2,000 human cases in Europe in 2018 (Bakonyi and Haussig, 2020) and more than 1000 cases in 2022 (ECDC, 2023). Coupled to that have been notable outbreaks of dengue virus (~2,000 human cases) in Madeira in 2012 (Wilder-Smith *et al.*, 2014), local autochthonous dengue cases in France in 2022 (Cochet *et al.,* 2022) in Italy and France in 2023, and two large outbreaks of chikungunya virus in Italy (~200 cases in 2007, >400 cases in 2017, Rezza, 2018). It is now quite expected that, each year, small clusters of dengue, chikungunya and occasionally Zika virus are reported in southern Europe. Although many of these emerging mosquito-borne arboviruses in Europe are confined to the warmer Mediterranean region, West Nile virus has now emerged in Germany (since 2018) and the Netherlands (since 2020) (Ziegler *et al.,* 2019; Vlaskamp *et al.,* 2020). Also in 2020, a small number of birds in London were found to be infected with Usutu virus (Folly *et al.,* 2020), and subsequent detection of the virus in local mosquitoes confirmed the first evidence of mosquito-borne virus transmission of potential public health significance in the UK (Lawson *et al.,* 2022).

This apparent change in distribution and increased incidence of mosquito-borne disease can be explained by many factors. Climate change and extreme weather events can facilitate the establishment of invasive mosquitoes, increasing the abundance of native and invasive mosquitoes and shortening the extrinsic incubation period for viruses that were previously considered as being tropical/sub-tropical (Medlock and Leach, 2015). Mosquitoes and viruses adapt to their surroundings, and increased transmission potential in a temperate climate is to be expected, particularly given the global movement of infected people from outbreak zones, back into Europe, a key factor in the spread of Covid-19.

The introduction of invasive mosquitoes (e.g. *Aedes* (*Stegomyia*) *albopictus* (Skuse, 1894), *Ae.* (*Stg.*) *aegypti* (Linnaeus, 1762)) into Europe and their rapid spread to ~30 European countries, has raised the prospect of emerging vector-borne disease on the emerging infection agenda. There are now genuine concerns that the climate of north-west Europe, including that of the United Kingdom, may in time, become suitable for local disease transmission (Schaffner *et al.,* 2013; Medlock *et al.,* 2017; Vaux *et al.,* 2020), as now appears to be occurring with Usutu virus (Lawson *et al.*, 2022).

These concerns come at a time of environmental change, and although invasive *Aedes* (*Stegomyia*) mosquitoes are not likely to be a risk in natural wetland systems, there are other species (including extant species) that may play a role in transmission of pathogens, such as West Nile virus, and that this may create a conflict with UK wetland management, creation and expansion. There is an increasing drive to create and enhance existing wetlands in the UK, as part of river and coastal flood alleviation, increased provision of wetlands for enhancing biodiversity, as well as ecological mitigation for development and increased urban blue-space (Committee on Climate Change, 2020; Defra, 2022a,b; Kumar *et al.,* 2017). The benefits of wetlands are manifold (Millennium Ecosystem Assessment, 2005), considered critical to the success of the Sustainable Development Goals (IPBES, 2017), and in the UK specifically have been highlighted by the Wetland Life project (Gearey *et al.,* 2020; Hawkes *et al.,* 2022). However, one key concern of local stakeholders has been the increasing risk posed by nuisance and vector mosquitoes in a warming climate, as wetlands can provide suitable aquatic larval habitat for many mosquito species. These opposing views can often be difficult to reconcile in the absence of empirical data or an informed response. There is therefore a need for greater awareness among the wetland management and environmental community in assessing the potential suitability of UK wetlands for mosquitoes, the impact of any management strategies, as well as preparedness planning in the event of an incursion of disease that merits local mitigation action.

This study aims to assist with tackling this conundrum, by generating further empirical evidence on British mosquitoes in a range of different wetland types across England, supplementing recent ecological studies on mosquitoes in English wetlands that were focussed in Cambridgeshire, coastal wetlands of eastern England and in newly created wetlands (Medlock and Vaux, 2011, 2013, 2014, 2015a,b). These data, along with other biological and ecological research and expert knowledge on British mosquitoes, will hopefully inform survey and risk assessment protocols for assessment, management and communication for wetland managers across the UK.

This paper presents the field sampling results for data on all British mosquito fauna in lowland England, including their phenology, that informed these mosquito predictions, which was made available as a series of flow charts to wetland managers in the *Wetland Mosquito Survey Handbook* (Hawkes *et al.,* 2020, part of the WetlandLIFE project). The empirical data that informed these flow charts are presented here, with results discussed in relation to functional groups of British mosquitoes and their distribution. The resulting flow charts are also included, but a detailed analysis of the decision tree predictions are not published here.

2 Materials and methods

As part of the WetlandLIFE project, over two years (2017–2018), field surveys were conducted at 12 wetland sites in England, via habitat surveys and sampling of both adult and larval mosquitoes. The field sites were categorised as either coastal re-alignment wetlands, wet-woodland dominated wetlands, remnants of established freshwater wetlands and urban wetlands, with three field sites chosen for each categeory. The reasons for these four categories were to ensure that the full range of mosquito diversity was captured. The coastal sites were chosen to capture brackish and coastal species, the wet woodlands sites to capture the not to woodland *Aedes* species, urban sites to cover sustainable urban drainage and urban wetland mitigation habitat and a final category that included some of the remnant wetland sites that have survived as relic wetlands from the main freshwater wetland systems (hereafter 'established freshwater wetlands') that existed before large-scale drainage and land use change. Trap-based adult sampling was conducted (where possible) for each wetland site, over one field season. At each each field site, the different types of aquatic habitat were classified and each sampled through larval surveys.

In order to assist with the development of the wetland mosquito predictions as part of WetlandLife, the first stage was to identify a list of generic aquatic habitat types that occur in English wetlands and begin to classify them in accordance with existing knowledge of mosquito life histories, building on the life history characteristics detailed in Medlock and Vaux (2015a,b) and the previous literature (Cranston *et al.*, 1987; Marshall 1938; Service, 1968, 1969, 1971, 1973, 1994; Snow, 1990; Medlock and Vaux, 2011, 2013, 2014, 2015a,b) on British mosquitoes, supplemented by ecological knowledge in Becker *et al.* (2010). Additional expert opinions from the authors were included through recent experience of dealing with specific issues relating to nuisance and vector mosquito species (e.g. *Ae. albopictus, Ae.* (*Aedimorphus*) *vexans* (Meigen, 1830)*, Ae.* (*Ochlerotatus*) *detritus* Haliday, 1833*, Culex* (*Barraudius*) *modestus* Ficalbi, 1890) arising through communications with wetland managers and local authority pest control officers, as well as species-specific research (Abbott, 2018; Golding *et al.*, 2012; Medlock and Vaux, 2015b; Medlock *et al.*, 2005, 2014, 2017; Rudolph *et al.*, 2020; Vaux *et al.*, 2015, 2019, 2021).

These generic aquatic habitat types, which are included in the survey handbook (Hawkes *et al.*, 2020), are shown in Figure 1. These aquatic habitat types were chosen based on the ecological, hydrological and management characteristics that are most relevant to aspects of mosquito ecology. These include permanence of water (as determined by timing and duration of natural or deliberate flooding), water movement (lotic or lentic), water salinity and degree of vegetation cover. In summary, these include permanent freshwater wetland habitats such as open mere/water, navigation drains/river and waterways, permanent ponds and semi-permanent scrapes (i.e. areas designed so that they will act as temporary ponds during periods of high rainfall and will slowly release water after flooding); transiently flooded freshwater habitats in wet woodland such as wet woodland pools, and wet woodland ditches; transiently flooded open freshwater habitats such as wet fen grassland, reedbed and acid bog/heath; coastal saline/brackish habitats such as salt-marsh, mud-flat and coastal drains; and other aquatic habitat types that can support mosquitoes in a wetland ecosystem, such as tree-holes.

Field validation and field sites

Twelve wetland sites were chosen as field sites (Table 1), with agreement from landowners for inclusion in the study. The aim was that field surveys would take place over two years (2017–2018) at six wetland sites in each year. During the first year, field data were collected from six wetlands: farm reversion, ditches, wet woodland, acid heath and reedbed at Shapwick Heath (SHP) and Westhay Moors in the Somerset Levels; valley mires, wet woodland and brackish saltmarsh at Arne (ARN) in Poole harbour, Dorset; flooded riverine and coastal habitat by the River Otter (OTT) in Devon; in urban country parks and wetlands at Priory Country park and Fenlake meadows in Bedford (BED), Bedfordshire; on coastal marshes at Northward Hill (NOR) in the North Kent marshes; and in fen and wet woodland habitats at

FIGURE 1 Classifications of wetland types according to British mosquito life-histories. Adapted from Hawkes *et al.* (2020).

Chippenham Fen (CHP) in the Cambridgeshire Fens. Exact locations and wetland particulars are presented in Table 1.

During the second year field sites were: Radipole Lake, adjacent to urban Weymouth (WEY) in Dorset; Alkborough Flats (ALK), a coastal realignment project along the River Humber in North Lincolnshire; wet woodland pools in Hurcott (HUR), Worcestershire; saltmarsh and estuarine habitat at Steart (STE) marshes in Somerset; flooded/wet grassland, fen, and wet woodland at Greywell Fen (GRE) in Hampshire; and at a sustainable urban drainage scheme in Milton Keynes (MLK) in Buckinghamshire (Table 1). At each site, all wetland habitats were initially appraised and discussions with

TABLE 1 Details of field study sites.

Site (wetland category)	Location	Lat Long	Size (ha)	Wetland description
Alkborough Flats (ALK; coastal)	North Lincolnshire	N 53.68 °, W 0.67 °	450	At the confluence of the rivers Trent and Ouse, on the south bank of the Humber estuary. Recently created coastal managed realignment site, created in 2006. Consists predominantly of low-lying mudflat, estuarine fresh/lightly saline water flooding with some freshwater ditches, scrapes, ponds and flooded grassland.
Arne (ARN); remnant wetland)	Dorset	N 50.68 °, W 2.04 °	>565	On the Arne peninsular of Poole harbour on the Isle of Purbeck. Wetland habitats include coastal saltmarsh and acid bog, with areas of wet woodland, woodland pools and coastal grazing marsh with freshwater ditches and flooded grassland.
Northward Hill (NOR; remnant wetland)	Kent	N 51.46 °, E 0.54 °	278	Located on and below a ridge overlooking and incorporating arable farmland and grazing marsh in the Thames estuary. Main wetland types are coastal grazing marsh, coastal ditches and flooded grassland, with proximity to other coastal habitats.
Radipole Lake (WEY; urban)	Dorset	N 50.62 °, W 2.46 °	83	In central Weymouth. It is dominated by reedbeds and saline lagoons and is bisected by the river Wey. Although surrounded by development on all sides, it is situated close to other coastal wetlands in Weymouth bay
Steart marshes (STE; coastal)	Somerset	N 51.19 °, W 3.07 °	~300	On the Steart Peninsula: edge of the Severn Estuary and River Parrett. A newly created coastal managed realignment site created in 2014 to create vast areas of new salt-marsh, mudflats and saline lagoons, with some areas of new freshwater wetlands
River Otter (OTT; coastal)	Devon	N 50.63 °, W 3.31 º	N/A	River rises in the Blackdown Hills, flows through Somerset/East Devon entering the English Channel at Lyme Bay. The lower reaches of the river, bordering Budleigh Salterton, include the Otter estuary nature reserve. With surrounding low-lying fields subject to a planned restoration project to create additional saltmarsh habitat, scrapes, saline lagoons, reedbeds and ditches
Shapwick Heath (SHP; remnant wetland)	Somerset	N 51.16º, W 2.82 °	500	Part of Avalon marshes in Somerset levels. Large area of flooded wetlands, formed following peat extraction, including wet woodland, large reedbeds, navigation ditches, flooded grassland and woodland/grassland ditches
Hurcott wood (HUR; wet woodland)	Worcestershire	N 52.40 º, W 2.21 º	35	Includes series of pools that provide wet woodland habitat.
Priory Park (BED; urban)	Bedfordshire	N 52.13 °; W 0.43 °	145	Greenspace on the edge of the town of Bedford, which includes meadows, reedbeds, small areas of wet woodland and is bounded by the River Great Ouse
Fenlake Meadows (BED; urban)			19	Nature reserve including wet grazing meadow
Chippenham Fen (CHP; remnant freshwater)	Cambridgeshire	N 52.29 °; E 0.42 °	117	Undrained, semi-natural calcareous fen with ditches, pools and wet depressions, with areas of woodland.
Greywell Fen (GRE; wet woodland)	Hampshire	N 51.25 °, W 0.97 °	13	Fenland, with fen meadow, wet woodland, inc, River Whitewater
Milton Keynes (MIL; urban)	Buckinghamshire	N 52.01 °, W 0.79 °	N/A	Small areas of sustainable urban drainage among urban housing estates

wetland managers followed, and a list of aquatic habitat types compiled (Table 2).

Field sampling

Mosquito Magnet® Executive mosquito traps (MosquitoMagnet, Lititz, PA, USA) baited with octenol (MosquitoMagnet) were run, where possible, every fortnight over four nights from week 14 to 44 (early-April to end-October). Traps were located as centrally as possible within each site, in somewhat sheltered environments to protect them from inclement weather and where there was minimum risk of vandalism or theft. Total adult female mosquito numbers for each trapping period are reported as the mean number per trap night n/TN). As traps were emptied at the end of each survey week, the mean was calculated from the number of mosquitoes collected during that survey period, divided by the number of trap nights. It was not possible to calculate standard error as individual nightly catches were not recorded. The numbers of mosquitoes by functional groups were also calculated in accordance with Figure 2. For each wetland, the various aquatic habitat types were categorised (Table 2). The numbers of trap nights and duration of sampling is summarised in Table 3. Also, at each field site, an example of each accessible aquatic habitat was surveyed for larvae (usually within 1–2 km of the adult trap): at each, 3 separate adjacent locations were sampled using a standard 250 ml dipper. At each larval sampling point 5×200 ml dips were taken and larvae were collected for later identification in the laboratory. They were stored in 70% ethanol to preserve morphological features. This was conducted three times during the year in May, July and September, and occasionally in March the following year. All mosquitoes were identified morphologically using the keys of Cranston *et al.* (1987), Snow (1990) and Becker *et al.* (2010). Where identification was not possible due to requiring DNA methods, species were grouped as follows: *Culex pipiens sensu lato* (*s.l.*) = *Cx.* (*Culex*) *pipiens* Linnaeus, 1758 and *Cx.* (*Cux.*) *torrentium* Martini, 1925; *Ae. cantans* = *Ae.* (*Och.*) *cantans* (Meigen, 1818) and *Ae.* (*Och.*) *annulipes* (Meigen, 1830).

Functional groups of British mosquitoes

In order to assist wetland managers in understanding the relative contributions of different aquatic habitat types to mosquito diversity and abundance, it was decided to introduce the concept of mosquito functional groups (Lundstrom *et al.*, 2013; Medlock and Vaux, 2015; Schäfer *et al.,* 2004), whereby mosquito species with similar life histories were combined to reflect the contributions of different aquatic habitat types to mosquito numbers. Figure 2 shows the various functional groups and their associated common species of British mosquito. Functional groups 1 and 2 are separated by the substrate that each mosquito lays their eggs (e.g. on water or land). These are further separated into their common overwintering stage and host, to leave 3 separate functional groups in FG1 (i.e. a-c) and 4 in FG2 (i.e. a-d). Aside from the tree hole aedines, all other aedines fall within FG2a

TABLE 2 Aquatic habitat types found at each of the 12 wetland field sites.[1]

Aquatic habitat types by wetlands	SHP	ARN	OTT	WEY	MIL	STE	BED	CHP	NOR	GRE	HUR	ALK
Wet grassland	■	■	■	■				■	■	■		■
Wet woodland pools	■	■		■			■	■		■	■	
Wet woodland ditches	■	■					■	■	■		■	
Open mere/water	■			■			■	■	■	■	■	
Reedbed	■		■	■	■	■	■	■		■		■
Permanent ditches	■	■	■	■		■	■	■	■			■
Navigation ditch/river	■		■	■			■		■			
Tree hole	■	■	■	■			■	■		■	■	
Acid bog	■	■										
Salt-marsh		■	■			■						
Mudflat			■			■						■
Coastal drain			■			■			■			■
Permanent pond/ scrapes			■	■	■			■	■	■		■

[1]WEY = Weymouth; SHP = Shapwick; NOR = Northward; STE = Steart; GRE = Greywell; HUR = Hurcott; OTT = Otter; CHP = Chippenham; BED = Bedford; ARN: Arne; ALK = Alkborough.

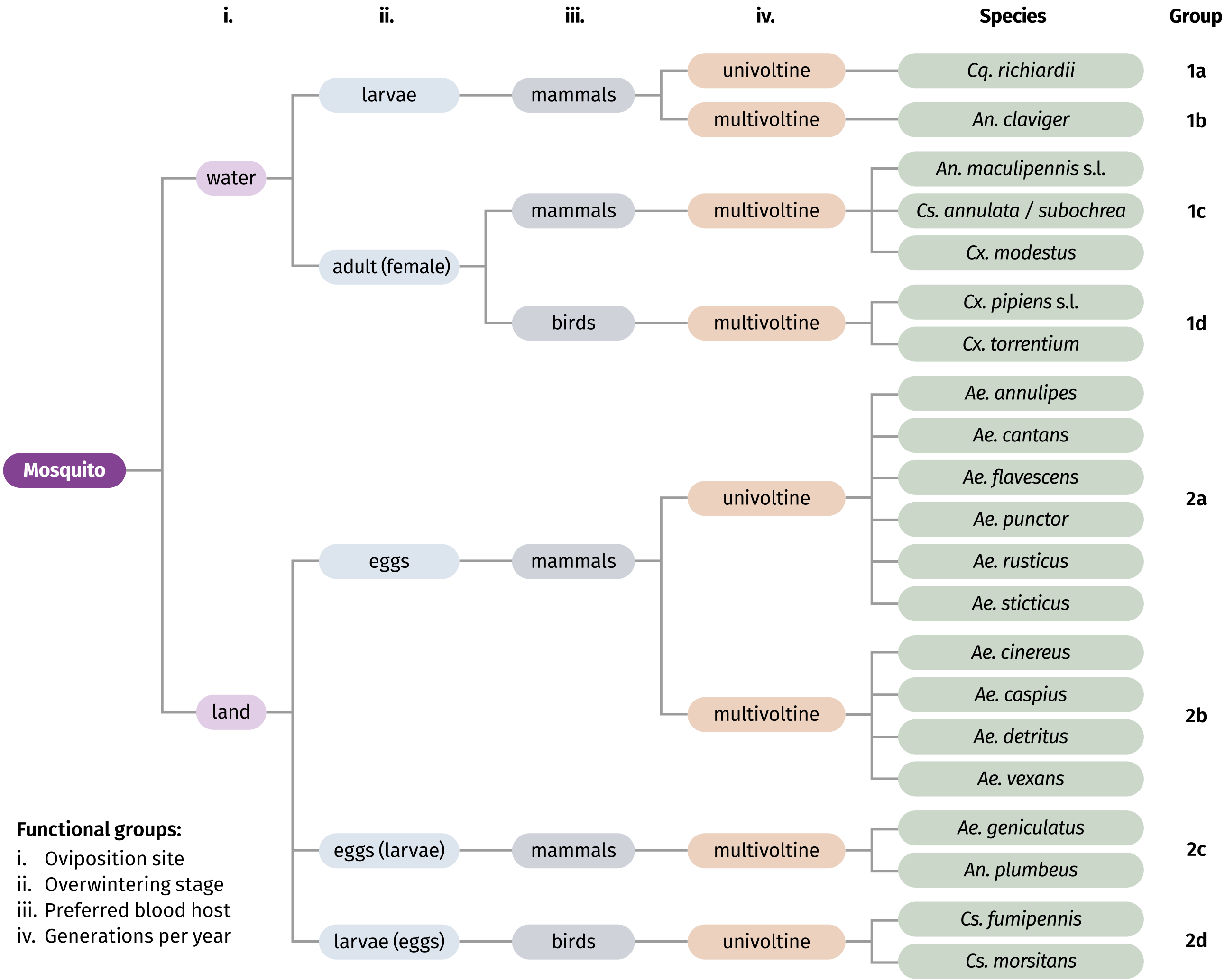

FIGURE 2 Functional groups of British mosquitoes according to their oviposition site, overwintering stage, preferred blood host and generations per year. Adapted from Medlock and Vaux (2015a), Hawkes *et al.* (2020).

[woodland flood-water species] and FG2b [open habitat flood-water species]. The data are therefore presented along these lines, to firstly highlight the key species that dominate by FG, and secondly to highlight the relative contributions of each FG to the four different aquatic habitat types of each wetland site.

To test associations between the mean densities of the main five species and whether they were associated with either inland and coastal wetland sites, Wilcoxon Signed-Rank Tests were conducted using an online tool at www.socscistatistics.com.

3 Results

In total, 38,577 female mosquitoes were collected from 21 traps during 905 trap nights at 12 wetlands, during the summers of 2017 and 2018. A total of 19 different mosquito species was collected (Figure 3, Table 4 and 5).

Mosquito functional group and species diversity: coastal versus inland sites

25,944 female mosquitoes were collected during 577 trap nights at the six coastal field sites (44.9/TN), and 12,633 during 328 trap nights at the inland field sites (38.5/TN). Functional group dominance varied between coastal and inland field sites, with FG 2b (open *Aedes* flood-water species) most common at coastal sites (~66% of all samples) and FG 2a (woodland *Aedes* flood-water species) most common at inland sites (~61% of all samples). Species from other FGs were trapped in similar proportions in both coastal and inland field sites, with 1a (*Coquillettidia* (*Coquillettidia*) *richiardii* (Ficalbi, 1889)) and 1b (*Anopheles* (*Anopheles*) *claviger* (Meigen, 1804)) accounting for 12.3–12.8% and 15.0–18.6%, respectively. Summaries of numbers of mosquitoes, stratified by functional group are shown by wetland type in Figure 4, and by field site in Figures 5 and 6 and Table 6, including indices on diversity, evenness and species richness. All

TABLE 3 Field sampling details: number of weeks of sampling, period of sampling (week numbers), numbers of trap nights per week and over the season.

Location (trap)[1]	Year of sampling	# weeks of sampling	Period of sampling (week numbers)	Numbers of trap nights per week	Total number of trap nights
ALK A	2018	7	16–35	7	49
ALK B	2018	7	21–35	7	49
ARN	2017	12	15–32	4 (3–7 for 3 wks)	49
BED A	2017	10	18–38	4 (7 for wk 20)	43
BED B	2017	8	18–38	4 (7 for wk 20)	35
CHP A	2017	14	16–42	3–4	53
CHP B	2017	14	16–42	3–4	53
GRE A	2018	6	20–34	4	23
GRE B	2018	4	20–28	4	15
HUR A	2018	6	20–30	4–5	25
HUR B	2018	3	20–30	4–5	13
NOR A	2017	14	20–43	4	52
NOR B	2017	9	20–41	4	37
OTT A	2017	4	20–29	4	15
OTT B	2017	6	16–38	4	24
SHP A	2017	5	20–28	4	20
SHP B	2017	12	16–42	3–5	48
STE A	2018	8	26–40	4	32
STE B	2018	12	21–40	4	50
WEY A	2018	17	21–41	7	110
WEY B	2018	11	21–31	7	110

[1] WEY = Weymouth; SHP = Shapwick; NOR = Northward; STE = Steart; GRE = Greywell; HUR = Hurcott; OTT = Otter; CHP = Chippenham; BED = Bedford; ARN: Arne; ALK = Alkborough. A and B represent the two different traps.

additional data on mosquito density and seasonality are shown for those wetlands with notable mosquito abundance in the supplementary file.

Open Aedes *flood-water mosquitoes* (*FG 2b*)

17,600 FG 2b mosquitoes were trapped, 76% were *Ae. caspius*, (n=13,439, accounting for 35% of all mosquitoes trapped, with 91% trapped at the coastal site of ALK). Although *Ae. caspius* were trapped in 16 of the traps, they were only found in moderate numbers (>10 individuals) in seven of the traps, and only 10 individuals were trapped at inland sites. The remaining FG 2b species consisted of *Ae. detritus* (15%, n=2,663), *Ae.* (*Aed.*) *cinereus s.l.* Meigen, 1818 (8.5%, n=1,495) and a small number of *Ae. vexans*. *Aedes detritus* was not collected at any inland site, with 78% of all specimens from STE, with notable populations present at other coastal sites except WEY and OTT. The highest densities of *Ae. cinereus* in coastal sites (or indeed anywhere) were in acid heathland/bog/woodland aquatic habitat at Arne (72%, 1,063/1,495). This species was the only FG 2b species found at any of the inland sites, present in good numbers (n=388) at CHP.

Woodland Aedes *flood-water mosquitoes* (*FG 2a*)

8,297 FG 2a mosquitoes were trapped, 91% of which were *Ae. cantans*, with the remaining species consisting of: *Ae.* (*Och.*) *flavescens* (Müller, 1764) (3.6%, n=305), *Ae.* (*Och.*) *punctor* (Kirby, 1837) (3.1%, n=260), *Ae.* (*Rusticoidus*) *rusticus* (Rossi, 1790) (1.3%, n=107) and *Ae.* (*Och.*) *sticticus* (Meigen, 1838) (0.4%, n=37). 90% of all *Ae. cantans* were trapped at SHP, a wet woodland site in the Somerset Levels, with very few trapped at any coastal site. It was the most common species at all three wet woodland sites (SHP, GRE, HUR). Although present at 9 sites (including all inland sites surveyed), apart from SHP, only CHP had notable numbers (n=65). *Aedes flavescens* was only present at the coastal site of ALK with *Aedes punctor* only found in coastal wetlands at ARN (where it was the dominant species). *Aedes rusticus*

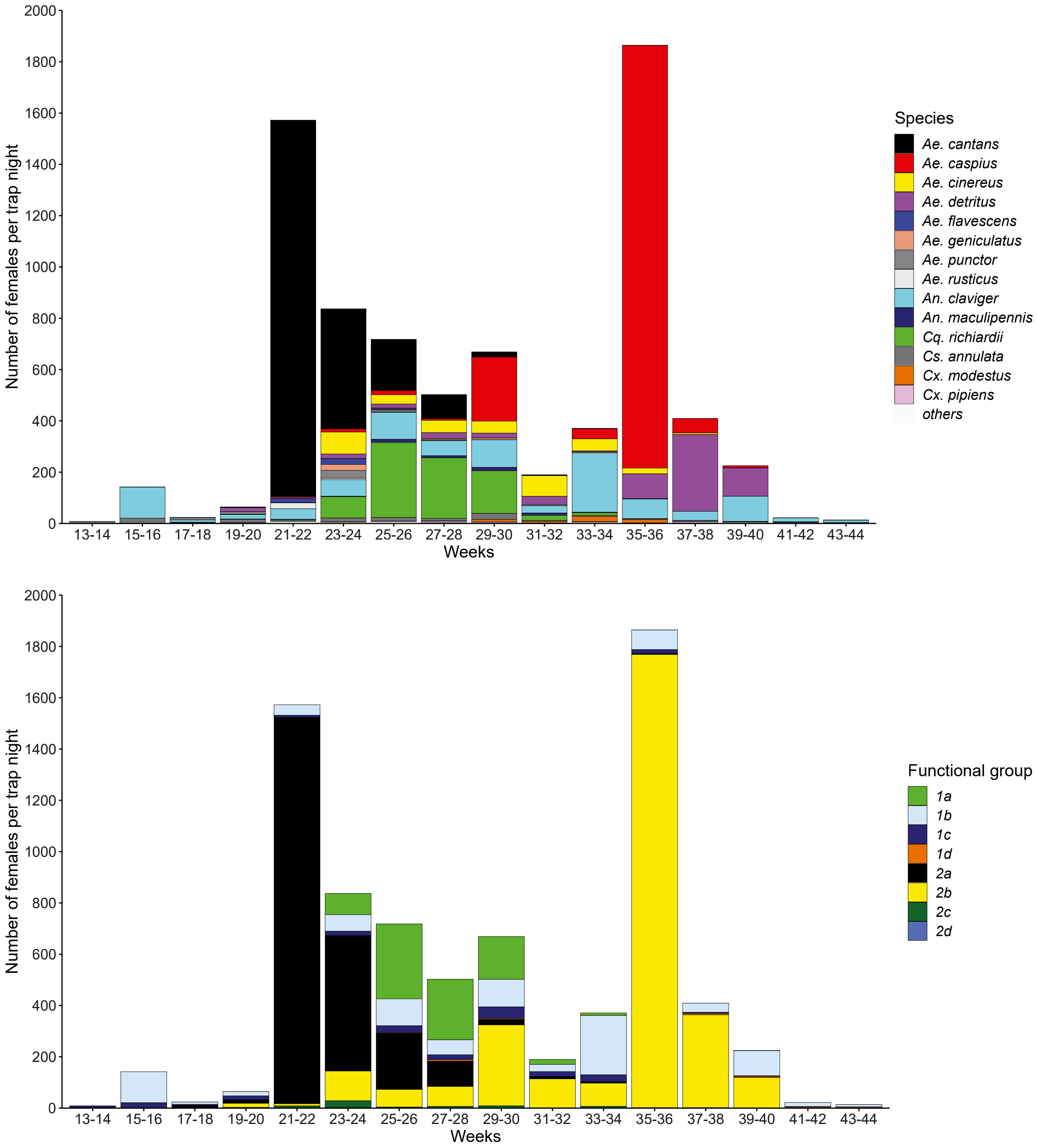

FIGURE 3 Seasonality of all mosquitoes collected by trap night, separated by (a) species and (b) functional group – refer to Figure 2 for detail.

TABLE 4 Numbers of female *Aedes* mosquitoes trapped during the study, separated by species and trap.[1]

Species	*Aedes cantans*	*Aedes rusticus*	*Aedes sticticus*	*Aedes punctor*	*Aedes flavescens*	*Aedes caspius*	*Aedes detritus*	*Aedes vexans*	*Aedes cinereus*	*Aedes geniculatus*
Funct.gp	2a	2a	2a	2a	2a	2b	2b	2b	2b	2c
Location										
SHP A	1,236	1								
SHP B	6,202	86								
GRE A	11	1								
GRE B	8	1							1	1
HUR A	30		22							2
HUR B	1									1
ALK A	5				208	1,838	24		3	
ALK B	3				97	10,432	146		7	
STE A						954	2,002			
STE B						73	67			
OTT A						14	1			
OTT B	2						1			
CHP A	22		13			3			387	104
CHP B	43	10	1						1	55
ARN				260		64	282		1,063	1
NOR A	1	8				43	130	1		
NOR B						6	1			
BED F	6		1			7		2	32	2
BED P	6									
WEY A	7					5	7		1	
WEY B	5						2			
Total by species	7,588	107	37	260	305	13,439	2,663	3	1,495	166
% all sp	19.67	0.28	0.10	0.67	0.79	34.84	6.90	0.01	3.88	0.43
# sites	16	6	4	1	2	11	11	2	8	7
>10/ site	6	2	2	1	2	7	6	0	3	2

[1] WEY= Weymouth, SHP= Shapwick, NOR= Northward, STE= Steart, GRE= Greywell, HUR= Hurcott. OTT= Otter, CHP= Chippenham, BED, Bedford, ARN= Arne, ALK= Alkborough.

was only common at the wet woodland site at SHP, and largely absent from all coastal sites, except a small number in the North Kent marsh site at NOR.

Functional groups 1a and 1b

Two-thirds (67%) of all mosquitoes trapped were from FG 2a and 2b. The next most trapped FG was 1b, which only contains *An. claviger* (n=6,240). This was one of the most ubiquitous mosquito species, found in every trap except one, and the dominant species at two coastal (WEY [52%, n=2,658], OTT [89%, n=549]) and two inland (CHP [67%, n=1,906), BED [67%, n=350]) sites. *Anopheles claviger* accounted for 15% and 18.6% of all individuals at coastal and inland sites, respectively. FG 1a only includes *Cq. richiardii*, which was trapped in every field site surveyed. It was found in relative abundance at both coastal (12.8% of all mosquitoes) and urban (12.3%) sites, although it was the dominant species only in grazing marsh habitat at NOR on the North Kent marshes (NOR: 54%, n=859).

Other functional groups

The remaining FGs only account for 3.7% and 4.7% of all mosquitoes at coastal and inland sites, respectively.

TABLE 5 Numbers of female mosquitoes other than *Aedes* spp. and total number of female mosquitoes trapped during the study, separated by species and trap.[1]

Species	*Coquillettid. richiardii*	*Anopheles claviger*	*Anopheles maculipen.*	*Anopheles plumbeus*	*Culex modestus*	*Culiseta annulata*	*Cuslieta subochrea*	*Culex pipiens*	*Culiseta morsitans*	Total for all FG by site[2]	% by site[2]
Funct.gp	1a	1b	1c	2c	1c	1c	1c	1d	2d		
Location											
SHP A	259	16	9	4		27		1	11	1,564	4.05
SHP B	1,070	73	16	4		106		16	9	7,582	19.65
GRE A	6			1		2				21	0.05
GRE B	4	3				2				20	0.05
HUR A	4	1				1				60	0.16
HUR B	2	1								5	0.01
ALK A	84	129	2			8		9		2,310	5.99
ALK B	33	465	2			34		7	2	11,228	29.11
STE A	85	12	8			1		24		3,086	8.00
STE B	35	15		1				3		194	0.50
OTT A	1	38		32		2		1		89	0.23
OTT B	3	511		2		3		6		528	1.37
CHP A	45	1,302		1		23			9	1,909	4.95
CHP B	153	604		23		62				952	2.47
ARN	47	45	1	5		50		20	1	1,839	4.77
NOR A	848	16	51	5	6	153		55		1,317	3.41
NOR B	11	1	36		197	8		1		261	0.68
BED F	3	347	36			50	1	4		491	1.27
BED P	4	3	6			7			3	29	0.08
WEY A	1,235	1,967	110	1		47		4	1	3,385	8.77
WEY B	946	691	48			11		4		1,707	4.42
Total by species	4,878	6,240	325	79	203	597	1	155	36	38,577	
% all sp	12.64	16.18	0.84	0.20	0.53	1.55	0.00	0.40	0.09		
# sites	21	20	12	11	2	19	1	14	7		
>10/ site	13	15	6	2	1	10	0	4	1		

[1]WEY = Weymouth, SHP = Shapwick, NOR = Northward, STE = Steart, GRE = Greywell, HUR = Hurcott. OTT = Otter, CHP = Chippenham, BED, Bedford, ARN = Arne, ALK = Alkborough.
[2]Total number of mosquitoes and percentage per site are including *Aedes* spp. (Table 4).

In FG 1c, *Cx. modestus* was only found in the North Kent marshes (n=203), *An.* (*Ano.*) *maculipennis s.l.* Meigen, 1818 (n=325) and *Culiseta* (*Culiseta*) *annulata* (Schrank, 1776) (n=597) occurred in 7 and 11 field sites, respectively, but were not dominant anywhere. FG 1d (*Cx. pipiens*, n=155) was found in low densities in all except three field sites (GRE, HUR, CHP), where they were absent. FG 2c (tree-hole species) were found in low numbers at many of the sites, with *An.* (*Ano.*) *plumbeus* Stephens, 1828 most numerous at OTT (n=34) and *Ae.* (*Dahliana*) *geniculatus* (Olivier, 1791) at CHP (n=159). Finally, FG 2d (*Cs.* (*Culicella*) *morsitans* (Theobald, 1901)) was not common anywhere, with the most found at the wet woodland sites at SHP (n=20).

Wetland type associations, densities and seasonality (adults & larvae)

Wet woodland dominant wetlands (*SHP, GRE, HUR*)

The three wet woodland sites had varying densities of mosquitoes. Only the wet woodland site (SHP) in the

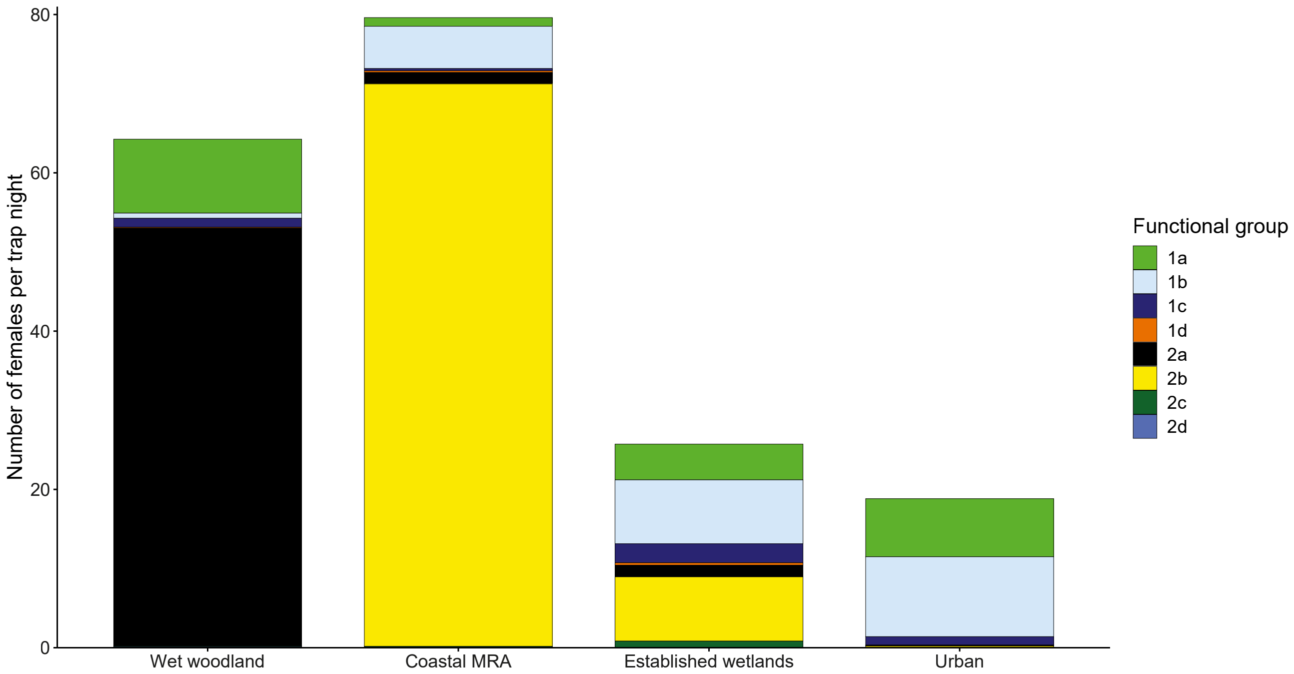

FIGURE 4 Numbers of mosquitoes per trap night, by wetland type and functional group. SHP, GRE and HUR are wet woodland sites; ALK, STE and OTT are coastal managed re-alignment wetlands, CHP, ARN, NOR are established wetlands from each of three distinct wetland systems; WEY and BED are urban wetlands. No mosquito trapping was conducted at MK. Refer to Figure 2 for details.

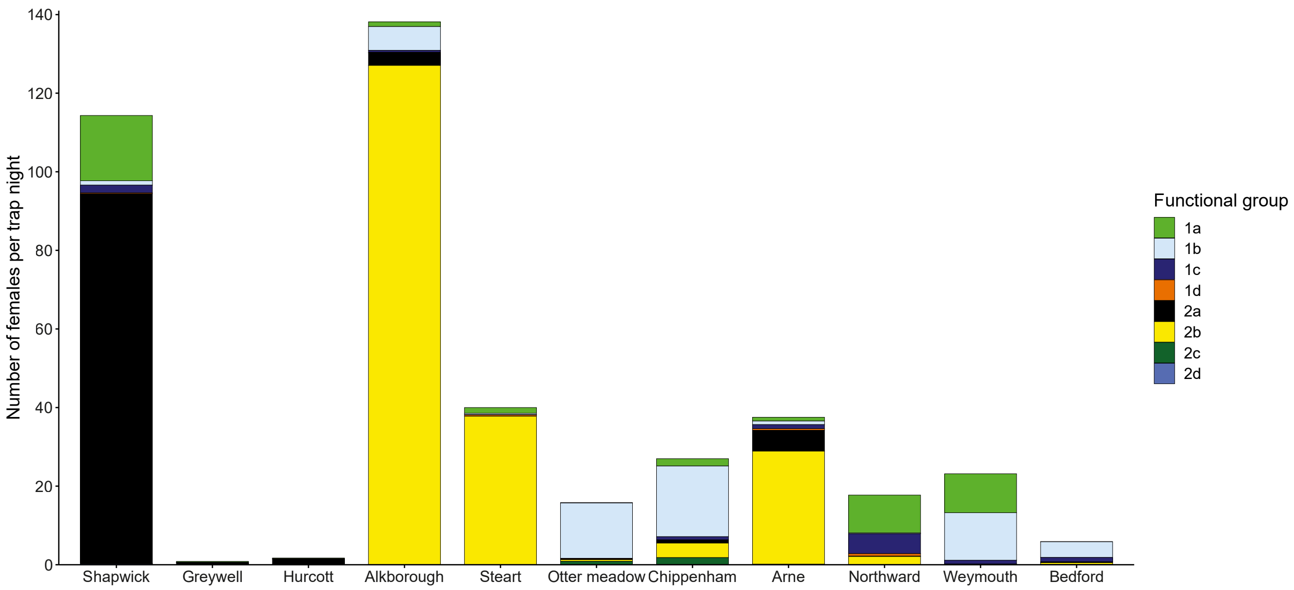

FIGURE 5 Numbers of mosquitoes per trap night, by wetland site and functional group. SHP, GRE and HUR are wet woodland sites; ALK, STE and OTT are coastal managed re-alignment wetlands, CHIP, ARN, NOR are established wetlands from each of three distinct wetland systems; WEY and BED are urban wetlands – refer to Figure 2 for details.

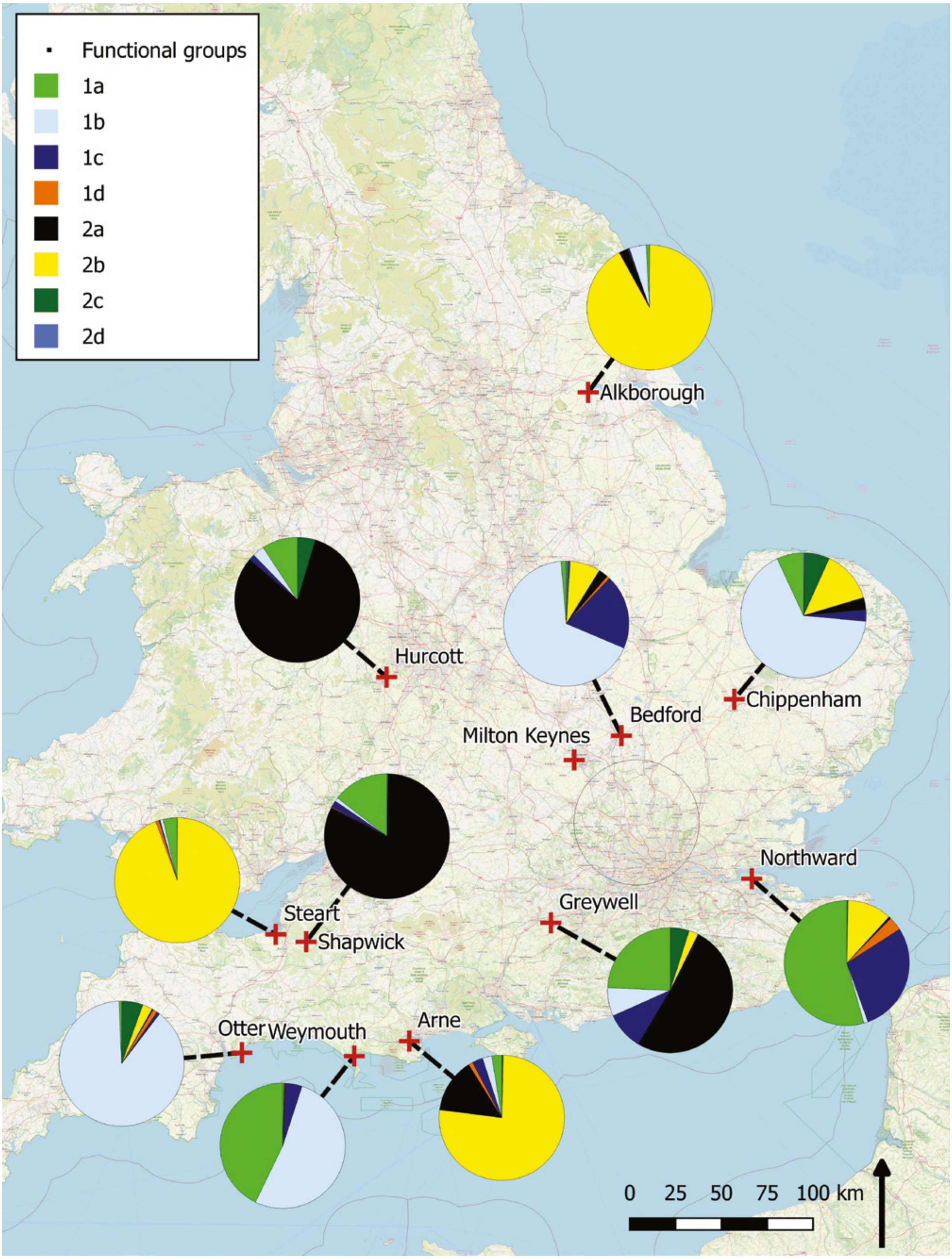

FIGURE 6 Comparison of functional group dominance by wetland location – refer to Figure 2 for details.

TABLE 6 Summary of mosquito collections, mosquito abundance, and diversity and evenness indices.[1]

Location[2]	Wetland category	# mosquitoes	Mosquitoes / trap night	FG (>20 individuals)	Species richness	Simpson (1-D) diversity index	Evenness
SHP	Wet woodland	9,146	134.5	7 (5)	9	0.32	0.294
GRE	Wet woodland	41	1.1	6 (1)	8	0.72	0.74
HUR	Wet woodland	65	1.7	5 (1)	6	0.66	0.699
ALK	Coastal MRA	1,3538	138.1	7 (5)	11	0.18	0.187
STE	Coastal MRA	3,280	40	6 (4)	8	0.5	0.42
OTT	Coastal MRA	617	15.8	7 (2)	8	0.2	0.245
CHP	Remnant wetland	2,861	27	7 (6)	11	0.53	0.496
ARN	Remnant wetland	1,839	37.5	8 (6)	12	0.62	0.546
NOR	Remnant wetland	1,578	17.7	7 (4)	12	0.66	0.613
BED	Urban	520	5.9	8 (3)	13	0.52	0.476
WEY	Urban	5,092	23.14	8 (3)	11	0.46	0.379

[1]FG = functional group. See Supplementary Materials for Shannon diversity index for all mosquitoes by month.
[2]WEY = Weymouth; SHP = Shapwick; NOR = Northward; STE = Steart; GRE = Greywell; HUR = Hurcott; OTT = Otter; CHP = Chippenham; BED = Bedford; ARN: Arne; ALK = Alkborough.

Somerset Levels had any great densities of woodland *Aedes*. *Aedes cantans* dominated the catch in the two years of survey (79% and 82%), with peaks in year 1 at week 24 (219.5/TN) and in year 2 at week 21 (1,465/TN). In both years, *Ae. cantans* remained at high densities until week 30 after which there was little activity. *Aedes cantans* was the most common species at GRE and HUR but at much lower peak densities (2–5/TN at weeks 26–30). It was also recorded in low densities at other, mainly inland sites, particularly if they also had areas of wet woodland. Populations at CHP peaked in week 28 (~10/TN).

Some other species were trapped in the wet woodland sites, with *Cq. richiardii* the next most common species, peaking at SHP in weeks 26–28 (26–159/TN). Other species were less common, with notable numbers of *Cs. annulata* (n=133), *Ae. rusticus* (n=86) and *An. claviger* (n=89) at SHP. At HUR, low densities (5/TN, week 26) of *Ae. sticticus* were trapped, with a low number of tree-hole species trapped at all sites. Wet woodland sites (SHP, HUR, GRE) were dominated by FG 2a species, constituting 82%, 87% and 51% respectively.

During larval sampling (Supplementary Table S1), a much broader range of species was collected at SHP than at other field sites. *Aedes cantans* was very common in woodland ditches and pools, particularly in May. *Culiseta morsitans* was found in the acid bog habitat in May, and in wet grassland, freshwater ditches, woodland ditches and pools and acid bog in March. Other species included *Cs. annulata, An. maculipennis* s.l., *Ae. cinereus* and *An. claviger*. Except for *Cx. pipiens* s.l. in ponds and scrapes, *Anopheles claviger* was the only other species found during larval sampling at GRE in scrapes, ponds, wet grassland and woodland pools. Larval sampling at HUR only detected *Cx. pipiens* s.l. and *Cs. annulata*, in woodland pools.

Coastal re-alignment wetlands (*ALK, STE, OTT*)
The three coastal field sites subject to recent or ongoing re-alignment schemes included ALK on the Humber estuary, OTT on the Devon coast, and STE on the Somerset coast of the Severn estuary. ALK and STE were both part of existing re-alignment schemes over the last 5–15 years and shared many similarities in mosquito

diversity, in contrast to OTT where new wetlands had not yet been created.

Functional group 2b dominates the trapped mosquitoes at ALK and STE, accounting for 92% and 94.4%. At ALK, the most common species caught was *Ae. caspius* (n=12,270; 90.6%), followed by *An. claviger* (n=594, 4.3%) and *Ae. flavescens* (n=305; 2.3%), with only low numbers of *Ae. detritus* (n=170, 1.3%). Seven other species were trapped in very low densities. *Aedes caspius* abundance remained low (<10/TN) until week 28, with abundance high by week 30 (185/TN) peaking in week 35 (early September; 1423/TN). *Aedes flavescens* peaked earlier in the year (week 21–24, 6–16/TN) with *An. claviger* present from weeks 21–35 at low densities (5–15/TN).

At STE, the most common species was *Ae. detritus* (n=2,069, 63.1%), followed by *Ae. caspius* (n=1,027, 31.3%) and *Cq. richiardii* (n=120, 3.7%), with five other species collected in very low densities. The peak for *Ae. detritus* (297/TN) occurred in weeks 38 at trap A (located by the saline marsh), about the same time as the *Ae. caspius* peak (137/TN, week 36). Densities for these two species were much lower (7/TN and 16/TN) at trap B (at the visitor centre, closer to the freshwater larval sampling points). The dominance of *Ae. detritus* at STE contrasted with the dominance of *Ae. caspius* at ALK. These two species were not trapped at OTT in any great abundance (16 in total). Here, FG 1b dominated, with *An. claviger* constituting 89% (n=549) of all mosquitoes trapped, with peaks in weeks 16 (114/TN) and 44 (8.8/TN). The only other notable species was a tree-hole species, *An. plumbeus* (n=34).

Coastal sites impacted by the tide, such as salt-marsh and mudflats, were mostly inaccessible. Larval sampling therefore was restricted to some of the fringe freshwater habitats, and this is reflected in the larval data (Supplementary Table S1). At ALK, no *Aedes* sp. larvae were detected, just small numbers of *An. maculipennis s.l.* and *Cs. annulata* in freshwater ditches and reedbeds. At STE, *Ae. detritus* were sampled in coastal ditches, with *Cx. pipiens* found late in the season in freshwater ditches. OTT had large numbers of *Cx. pipiens* in wet grassland aquatic habitats on all three visits, with *An. claviger* larvae present in September.

Established wetlands (CHP, ARN, NOR)

Three field sites were chosen as examples of wetlands representing fen, ditch and acid heath habitat, located within three different large wetland systems. These included Chippenham Fen (CHP) in the Cambridgeshire fens, Northward Hill (NOR) in the North Kent Marshes and Arne (ARN) in Poole harbour. Compared to some of the wet woodland and coastal realignment wetlands, where only 6–8 species were trapped, in these wetlands, 11–12 species were trapped, usually in much higher densities.

The three field sites were each dominated by different species. CHP, an inland fen wetland, was dominated by *An. claviger* (n=1,906, 67%; active from weeks 18–42, peaking in weeks 30–40 [50–81/TN]), and *Ae. cinereus* (n=388, 13.5%; no activity before week 24, peaking in week 36 [19.6/TN]); species typical of fen and wet grassland habitat. There were notable densities of *Cq. richiardii* (n=198, 6.9%; 10–15/TN in week) and *Ae. geniculatus* (n=159, 5.5%; 15.4/TN peak in week 24), with lower densities of *Cs. annulata* and *Ae. cantans*. The dominant FG at CHP was 1b (66.6%) and 2b (13.7%).

ARN, a coastal field site with acid heath, was dominated by *Ae. cinereus* (n=1,063, 57.8%; no activity before week 24, peaking to 26–80/TN in weeks 24–32), *Ae. detritus* (n=282, 15.3%, peaks in weeks 24–28 [13/5/TN] and week 32 [31.8/TN]) and *Ae. punctor* (n=260, 14.1%; peak in week 24 [31/TN]); all species typical of acid and salt-marsh habitats. Other notable species included *Ae. caspius*, *Cs. annulata, Cq. richiardii* and *An. claviger*. The dominant FG at ARN was 2b (76.6%) and 2a (14.1%).

NOR was typical coastal grazing marsh in an area of England known for *Culex modestus*. The dominant species were *Cq. richiardii* (n=859, 54.4%; peak in weeks 27–29 at 80–92/TN), *Cx. modestus* (n=203, 12.9%; peaking in weeks 29–35 at 19.3/TN), *Cs. annulata* (n=161, 10.2%; (weeks 20–29, peaking at 11–14/TN) and *Ae. detritus* (n=131, 8.3%; peaks in weeks 20–29 at 10–13/TN). Other species including *An. maculipennis s.l.* were also at notably low abundance. The dominant FG were 1a (54.4%) and 1c (28.6%).

In these established wetland field sites, five species were common to all (*Ae. caspius, An. claviger, An. plumbeus, Cq. richiardii* and *Cs. annulata*). *Aedes detritus* was only found in the two coastal sites, *Ae. punctor* only in the acid heath/woodland aquatic habitat, *Cx. modestus* only in the grazing marshes. *Aedes cinereus* was more common in the acid woodlands at ARN, but also found at NOR.

During larval sampling (Supplementary Table S1) at CHP, *Cx. pipiens* s.l. and/or *Cs. annulata* were found in a variety of habitats including woodland ditches and pools and wet grassland; *An. maculipennis s.l.* and *An. claviger* in freshwater ditches, and *An. maculipennis s.l.* in wet grassland. Similar established wetland associated species were found at NOR. ARN had a different assemblage of larval species, with >900 larvae collected during sampling. The largest proportion of these were *Ae. detritus* in salt-marsh in May and September, *Ae. cinereus* in acid bog and acid pools in May, *Ae. punctor* in woodland pools and woodland ditches in March and May, *Ae. caspius* in woodland pools and ditches in May, with small numbers of *An. maculipennis s.l., Cs. annulata* and *Cx. pipiens s.l.* in freshwater ditches, wet grassland and acid bog in July and September.

Urban wetlands (MLK, BED, WEY)
The remaining three field sites were examples of urban wetlands. At the Bedford wetlands, no mosquito species were common, although these wetlands had the greatest number of species (n=13). Only *An. claviger* (n=350, 70%; peaks at 26–28 and 36 at 19–40/TN) was common, with notable numbers of *An. maculipennis s.l.* and *Cs. annulata*. All other species were at low densities. WEY was a much larger wetland, dominated by reedbeds. Two species dominated the catch: *An. claviger* (n=2,658, 52%; peaking in weeks 39–41, 44/TN) and *Cq. richiardii* (n=2,181, 43%; peaking in weeks 25–27, 36/TN). Only *An. maculipennis s.l.* and *Cs. annulata* had notable populations. FGs 1a and 1b dominated at WEY (95%) and 1b (67%) at BED. Owing to restrictions it was not possible to run any adult traps in the Milton Keynes sustainable urban drainage wetlands, but larval sampling elicited no evidence of mosquitoes.

Larval sampling (Supplementary Table S1) at BED elicited low larval densities of a variety of species, with *An. maculipennis s.l., Cx. pipiens s.l., Cs. annulata* found in freshwater ditches and ponds, *An. claviger* in freshwater ditches, and *Cx. pipiens s.l.* and *Cs. morsitans* in reedbed. Three ubiquitous species (*Cx. pipiens s.l., Cs. annulata, An. maculipennis s.l.*) were collected at WEY in woodland pools, reedbed and waterways, with *An. claviger* also found in the reedbed. During larval sampling at MLK, no mosquitoes were found.

Summary
Based upon the surveys conducted here, five or six species were commonly collected in the adult traps. Early summer (weeks 21–28) collections were dominated (in wet woodland habitats) by woodland *Aedes* species (*annulipes/cantans*). Later in the summer (weeks 29–36) *Ae. caspius* is abundant in coastal estuarine and wet grassland habitats. *Aedes detritus* was also common in brackish habitats in coastal areas at a similar time (weeks 35–40). Other species, such as *Cq. richiardii* and *An. claviger* are ubiquitous but rarely highly abundant, with the former having a defined peak (weeks 23–30) and the latter present for the longest period across the season (weeks 16–44). These five species groups accounted for 90.2% of all individuals trapped, with *Ae. caspius* alone representing ~35% of all adult female mosquitoes trapped, followed by *Ae. annulipes/cantans* (19.7%), *An. claviger* (16.2%), *Cq. richiardii* (12.6%), and *Ae. detritus* (6.9%). To test associations between the mean densities of the main five species and whether they were associated with either inland and coastal wetland sites, Wilcoxon Signed-Rank Tests were conducted. Neither *Cq. richiardii* (w = 22, z = −0.56, P>0.05) nor *An. claviger* (w = 19, z = −0.866, P>0.05) were significantly more abundant in inland versus coastal sites. In contrast, *Ae. annulipes/cantans* (w = 1, z = −2.7, P=0.007) were significantly more abundant at inland sites. There were too few records of either *Ae. caspius* or *Ae. detritus*, to complete an accurate test, suggesting that they are both coastal species. When analysis was conducted at a functional group level (only including species where >300 individuals were collected in total: i.e. 8 species, 96.5% of all specimens), functional groups 1a, 1b and 1c were not significantly more associated with either inland or coastal sites. FG 2a were significantly associated with inland sites (P<0.05) although FG 2b, whilst weakly associated with coastal sites (w = 10, z = −1.78, P=0.075), this was not significant.

4 Discussion

For many wetland managers and those involved in habitat creation and management, the prospect of creating an environment that enhances the risk of mosquito development and subsequent mosquito biting is always a concern. This is likely to be ever more important when considering wetlands in the context of environmental change, where the prospect of disease emergence is possible, particularly in those situations where human exposure to mosquitoes through the proximity to wetlands is particularly proximal or is likely to increase through urban expansion or land use change.

Until now there has been very little openly accessible information for wetland managers to access the body of research on mosquitoes and wetlands in the UK, despite there now being a small number of relevant research papers (e.g. Medlock and Vaux, 2015b) that have attempted to address this key issue. This makes evidenced-based responses to mosquito-related concerns a real challenge for wetland managers. There is a wealth of information on the benefits and management of wetlands for a range of other invertebrates (Kirby, 2001), but often the Culicidae are seen as an inconvenient by-product in the case of some wetlands, and in general they engender very little enthusiasm even among entomologists, never mind wetland managers or the public: at one of our study sites, a wetland manager lamented that despite being aware that mosquitoes were present on the site they managed, no Culicidae had ever been formally included in species lists and were almost not considered to be a part of our native biodiversity.

The development of the *Wetland Mosquito Survey Handbook* (Hawkes *et al.,* 2020) was an attempt to dispel the myths about mosquitoes, set them in context with the wider food-web and aquatic habitat types in wetlands and provide accessible survey guidance and knowledge for further site-specific assessment. However, to achieve something that could be classed as generic prediction flow charts, there needed to be some empirical data to supplement the body of scientific literature on British mosquitoes.

From this study what is clear is that permanent wetland habitats, including those promoted through the creation and regular management of ditches, ponds and large open areas of water (e.g. meres) tend not to support large densities of mosquitoes, and there is little evidence that these habitats cause nuisance species (Medlock *et al.*, 2012). It has already been suggested that healthy wetlands can control mosquitoes (Medlock and Vaux, 2011), and there is evidence that a range of vertebrate and invertebrate predators can control mosquitoes in healthy permanent water wetlands (Medlock and Snow, 2008), provided that they are not affected by drought or nutrient enrichment. The mosquito prediction flow chart for open water and waterways is shown in Figure 7.

There are, however, three key generic wetland categories that do support mosquitoes, sometimes leading to high densities of pest species, and these are coastal habitats (Clarkson and Enevoldsen, 2020; Medlock and Vaux, 2013), wet woodland and wet/flooded grassland (Medlock and Vaux, 2015a; Vaux *et al.*, 2021), and therefore it is important to fully understand the factors that determine mosquito species assemblage and densities. The aquatic habitat types in these wetland categories contribute the greatest densities of mosquitoes, but there are complexities, and the suitability of each wetland site for these species varies, making any assessment conducted requiring a site-specific assessment.

During this study there were six coastal habitats studied. Two of the sites: Alkborough and Steart, had many commonalities, in that they were relatively recently created coastal re-alignment sites on England's largest estuaries (the Humber and Severn respectively), and are consequently subject to tidal flooding. Steart marshes are located at the mouth of the River Parrett as it meets Bridgwater Bay beyond the range of the Severn estuary in the Inner Bristol Channel, and so there is a mixture of riverine freshwater and coastal brackish water. In contrast, Alkborough flats lies at the confluence of the rivers Ouse and Trent, at the head of the Humber estuary, and so the brackish influence is much reduced, and most of the tidal flooding is riverine freshwater. Two key species: *Ae. detritus* and *Ae. caspius* dominate these coastal habitats, and it seems likely that the relative proportions vary based upon the salinity of the water, with *Ae. detritus* preferring more saline waters and *Ae. caspius* found in more estuarine and freshwater flooding, although Becker *et al.* (2010) reports that both are halophilic species, but that *Ae. caspius* regularly breeds in freshwaters with 0.5 g NaCl/L (Pires *et al.*, 1982) and can breed in large numbers in floodplains (Becker *et al.*, 2010). Other UK studies have reported *Ae. detritus* populations in brackish salt-marsh on the Dee estuary in Cheshire (Clarkson and Enevoldson, 2020), Sandwich (Ramsdale and Snow 1995) and previously on the Humber at Welwick (Medlock and Vaux, 2013), with *Ae. caspius* found in high numbers inland in freshwater flooded grassland in Cambridgeshire (Medlock and Vaux, 2015a) and in low saline areas at the head of the Humber estuary (Medlock and Vaux, 2013). Another floodwater coastal species, *Ae. flavescens* can be found and was recorded in lower numbers at Alkborough. This species is coastal and can tolerate salinity up to 50% sea water (Service and Smith, 1972).

Larval sampling of these habitats to detect these species can be difficult as the inaccessible nature of the salt-marsh or mudflat habitats make larval sampling very difficult or impossible (Medlock and Vaux, 2013). Sampling may be possible at the margins of the coastal habitat, but there may be a tendency to survey adjacent freshwater habitats that are co-created, and these will describe a different assemblage of mosquitoes to those that dominate in the wetlands of the intertidal zone.

The other four coastal wetlands, that were not impacted as much by the tidal regime, provided a different assemblage of mosquitoes. Arne, in Poole harbour, is an acid heath and bog habitat with marginal salt-marsh. *Aedes cinereus* occurred in the acid bog and margins of the wet grassland, and high densities of larval *Ae. detritus* in the salt-marsh. The acid pools in the wet woodland at Arne were exploited by large numbers of larval *Ae. cinereus*, accompanying the expected *Ae. punctor*.

The coastal habitats of the River Otter in Devon, and Radipole Lake in Dorset were both dominated by *An. claviger*, largely associated with summer flooded open habitat, and this seems to be a common species of a range of fen and wet grassland habitats. However, it is

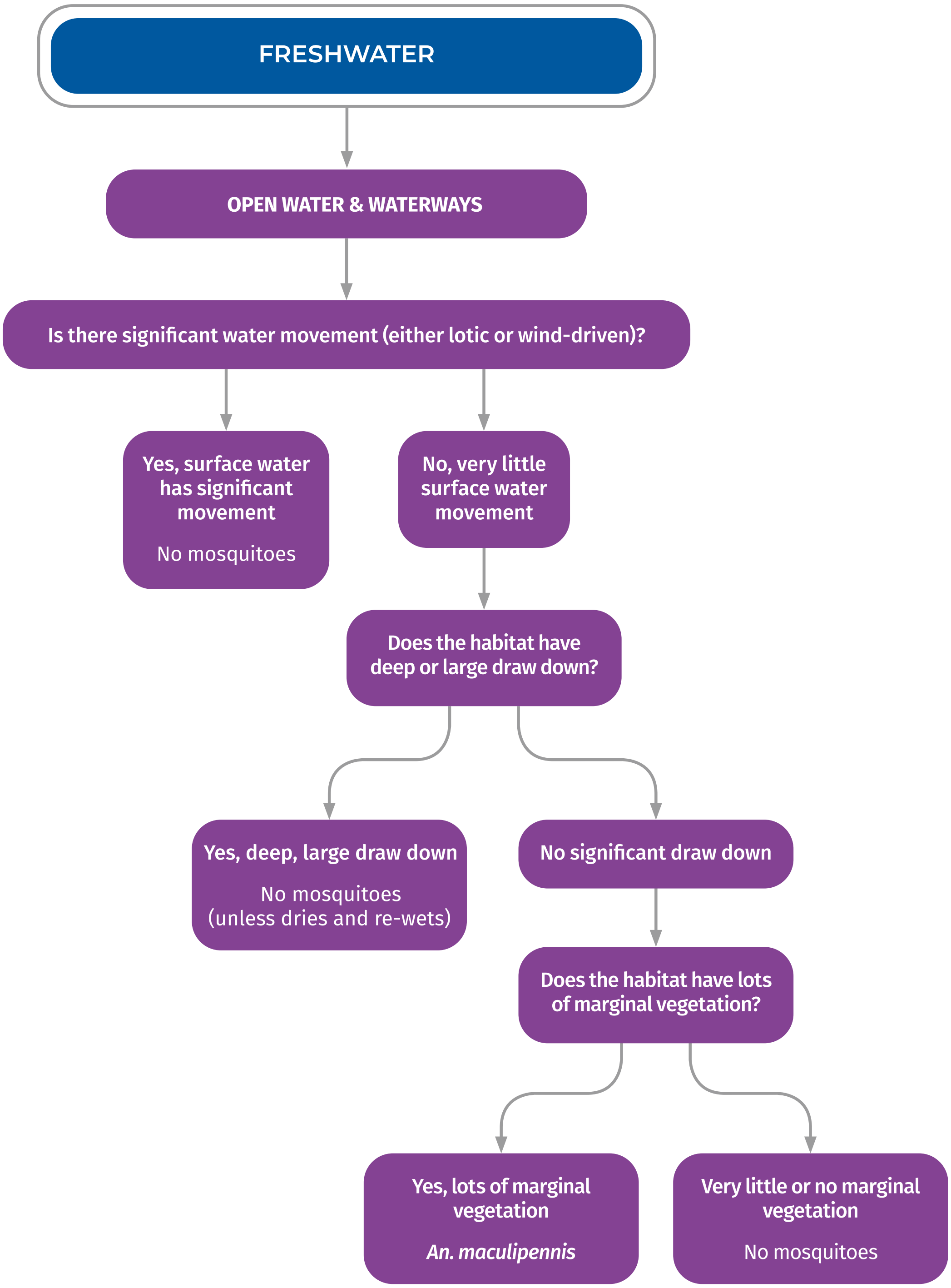

FIGURE 7 Mosquito prediction flow chart for open water and waterways. Adapted from Hawkes *et al.* (2020).

known to occur in brackish water with salinity up to 36% with a preference for cool water <20 °C, thus preferring shade, and usually in permanent waters (Becker *et al.*, 2010; Cranston *et al.*, 1987), with a bivoltine life history (Service, 1973). This species, along with *Cq. richiardii* in reedbed at Weymouth, dominated these wetlands. The lack of flooding of adjacent wet grassland at Weymouth during the study period may have led to absence of *Ae. caspius*, which would normally have flourished if it had flooded. The River Otter site is currently subject to a re-alignment scheme, and although no larval *Ae. detritus* was detected in the salt-marsh, this species, along with *Ae. caspius*, may colonise in the future, dependent upon salinity and extent of tidal flooding.

Northward Hill was included in the study as from previous mosquito surveillance, the area of the North Kent marshes has populations of *Cx. modestus* mosquitoes. Details of their range have been published elsewhere, and so far, the main populations are in North Kent and coastal Essex (Abbott, 2018; Medlock *et al.,* 2018; Vaux *et al.,* 2015), with a small population recently identified in Cambridgeshire (Welch, 2021). Interestingly, during the larval sampling no *Cx. modestus* were detected, and only one of the two traps had notable populations, suggesting that this species can easily be overlooked, even within and adjacent to sites where they occur. The mosquito prediction flow chart for brackish/coastal habitats is shown in Figure 8.

Several of the field sites had some wet woodland, but few mosquito species dominated in this habitat. *Aedes annulipes/cantans* dominated at Shapwick Heath and is the most common species of wet woodland habitat. However, in acid soils, such as those found at Arne, *Ae. punctor* is common, and *Ae. cantans* was absent. Marshall (1938) reported that *Ae. punctor* breeds almost exclusively in sandy and gravelly soil, such as in heath or woods where pine or birch trees predominate, with a distinct preference for acid pools. *Aedes cantans* is not reported to be acidophilic (Becker *et al.*, 2010; Cranston *et al.*, 1987) but larvae are reported to occur with *Ae. punctor*. This paper does not differentiate between *Ae. annulipes* and *Ae. cantans* on account of their morphological similarity. Marshall (1938) reported that *Ae. annulipes* is found in open, or only partly shaded situations, with *Ae. cantans* almost always selecting densely shaded ones. He reported that they were never found breeding together, but more recent studies summarised by Becker *et al.* (2010) suggests otherwise.

The presence of *Ae. cinereus* in these acid woodland pools confirms the reports by Becker *et al.* (2010) that

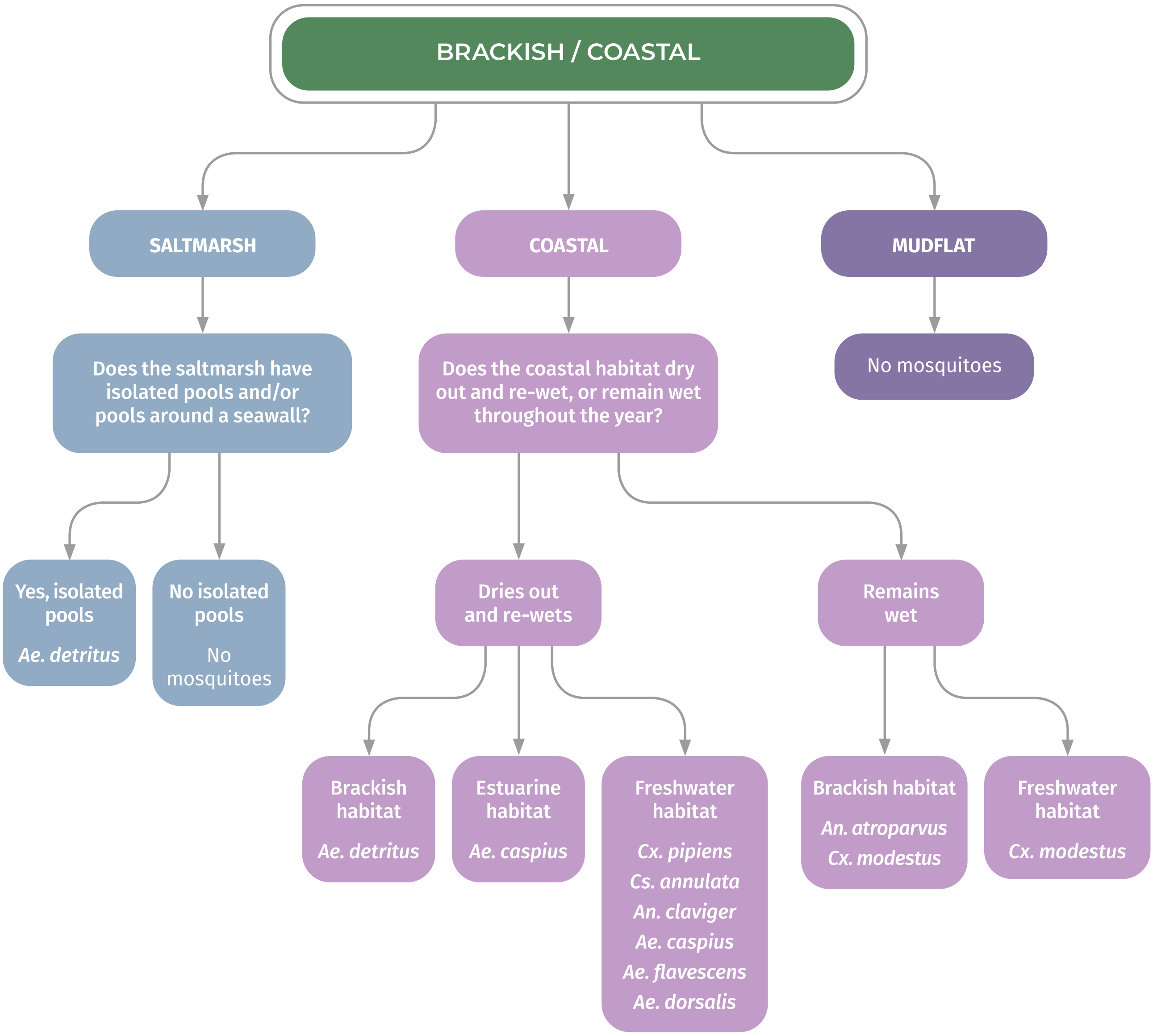

FIGURE 8 Mosquito prediction flow chart for brackish/coastal habitats. Adapted from Hawkes *et al.* (2020).

this species is acidophilic. At Hurcott, a site noted for its populations of *Ae. sticticus,* this under-recorded species was quite common, although Cranston *et al.* (1987) reports it as being a rare species in the UK. The abundance of wet woodland species can vary between years, depending upon the amount of winter and spring flooding. For example, very few woodland *Aedes* were reported at Greywell, but they are known to be common in wet years. Hurcott experiences flash flooding as well as management of groundwater levels to ensure that the wet woodland remains wet, and so this needs to be borne in mind when sampling. The mosquito prediction flow chart for wet woodland habitat is shown in Figure 9.

Wet/flooded grassland species can be extremely abundant, and cause considerable biting nuisance, as evidenced by a recent paper on *Ae. vexans* in a flooded

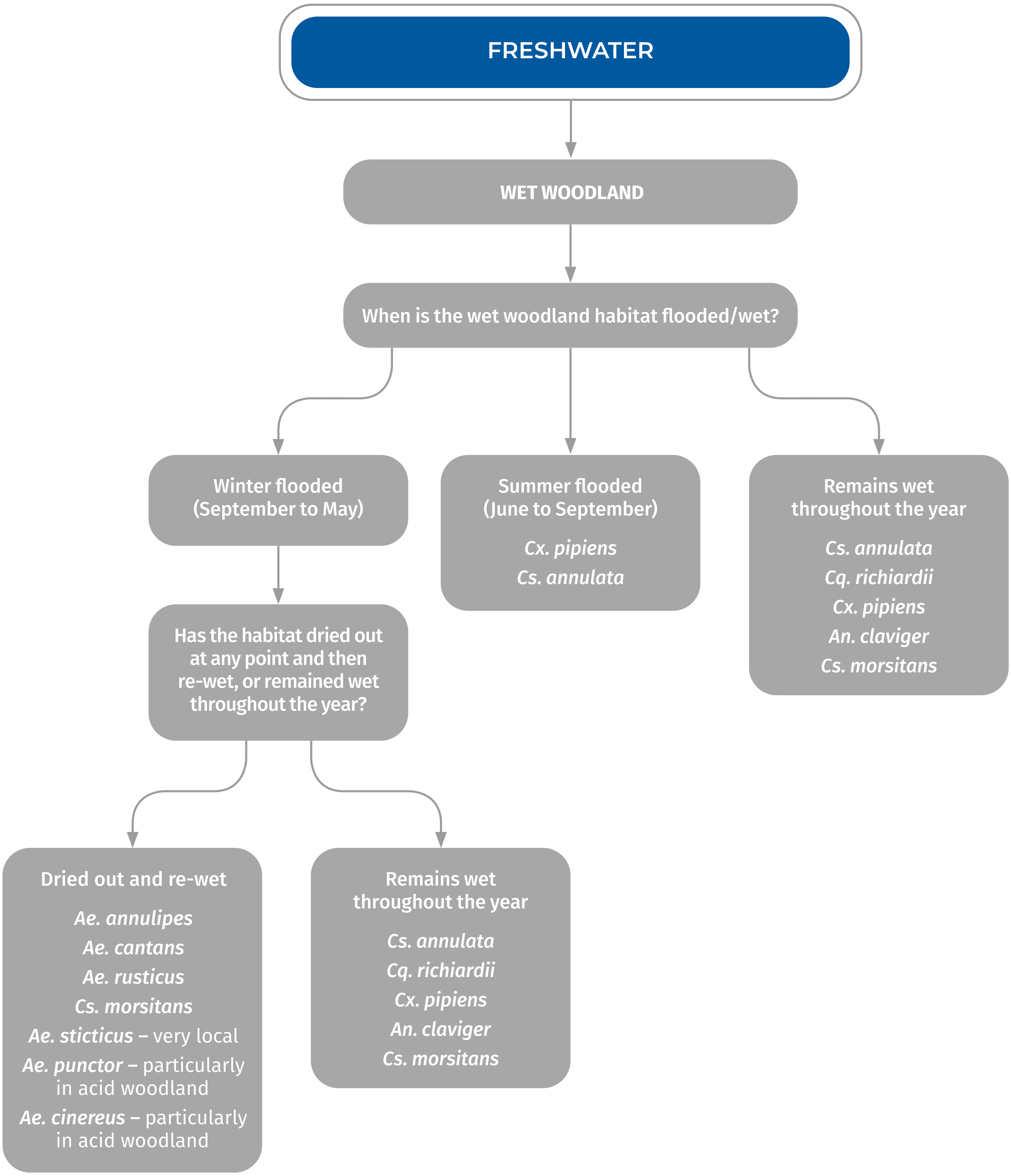

FIGURE 9 Mosquito prediction flow chart for wet woodland. Adapted from Hawkes *et al.* (2020).

river system in Nottinghamshire (Vaux *et al.*, 2021). This species is not common in the UK, and so is not currently expected in all summer flooded grassland aquatic habitat, but it can be highly abundant and a serious pest (Becker *et al.*, 2010). Previous work in the Cambridgeshire fens reported high densities of *Ae. cinereus* and *Ae. caspius* in flooded grassland and fen (Medlock and Vaux, 2015a), but there was little evidence of this at any of the sites surveyed. It could be due to the lack of grassland flooding during the surveys or that these species occur focally. What was clear was that in flooded grassland and fen habitat, *An. claviger* is common, but never very abundant. The mosquito prediction flow chart for wet grassland and freshwater ditches is shown in Figure 10.

From the surveys of the 12 field sites, five or six key species appear to be most common in the adult traps. These included an early summer peak of high densities (in some locations) of *Ae. annulipes/cantans* during weeks 21–-28, and these are a nuisance species associated with wet woodland (Becker *et al.*, 2010). Later in the year, *Ae. caspius* can be equally abundant from weeks 29–36 in coastal estuarine and possibly wet grassland habitats. *Aedes detritus* remains the most common species of brackish water habitats, with the largest peak in late summer (weeks 35–40), as supported by Clarkson and Enevoldson (2020). Other notable species are *Cq. richiardii* in reedbed and ditch habitat in a defined single peak during weeks 23–30, with *An. claviger* perhaps the most commonly recorded species throughout the year, recorded in all active sampling weeks from 16–-44, but never very abundant, and not necessarily associated with nuisance biting.

There are other species, such as *Cx. pipiens s.l.* which are commonly found during larval sampling, and given that this is a pioneer species, it is able to exploit a range

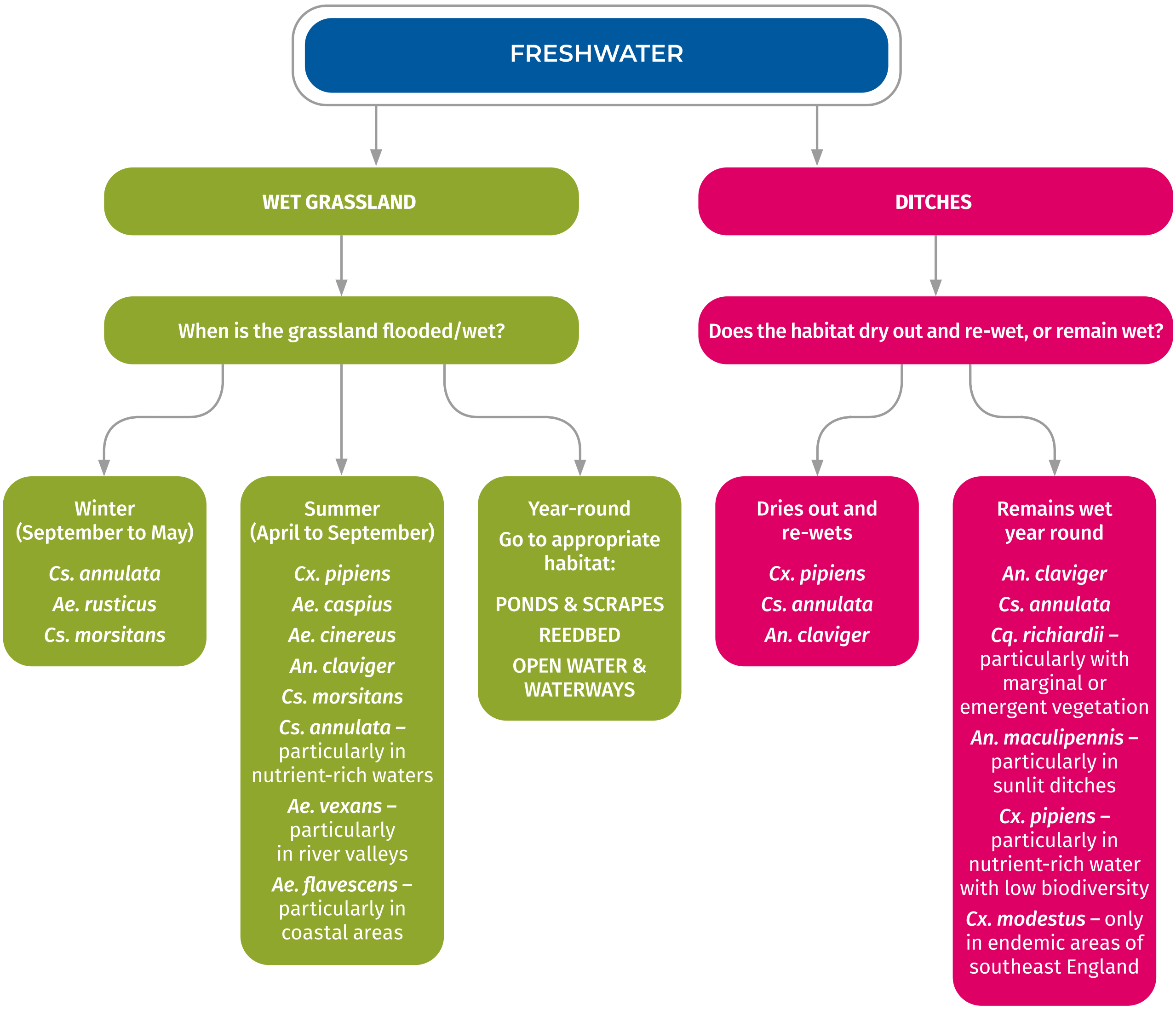

FIGURE 10 Mosquito prediction flow chart for wet grassland and freshwater ditches. Adapted from Hawkes *et al.* (2020).

of habitats (Cranston *et al.*, 1987). However, unless they are the *molestus* form, they do not generally get trapped in the Mosquito Magnet trap with a mammal lure (octenol). *Culiseta morsitans* is another under-recorded species in adult traps, but some of them were found in woodland ditches and pools (as previously recorded by Medlock and Vaux (2015a)) and acid bog habitat. The mosquito prediction flow chart for acid bogs, ponds and scrapes, reedbed and tree holes is shown in Figure 11.

The data generated here have been used to inform flow charts that are intended to assist with making predictions of species assemblages in a wetland, based upon the functional groups outlined previously. Ultimately though abundance of these species will be dictated by the prevailing weather and the local idiosyncrasies of water and vegetation management, as well as tidal regimes. There were some species that tend to be unusual but are highly abundant where they occur in the UK, such as areas with *Cx. modestus*, localised foci of *Ae. vexans*, or records of species that are under-recorded, such as *Ae. sticticus* and *Cs.* (*Cus.*) *subochrea* (Edwards, 1921). These empirical data which inform the Wetland Life mosquito handbook (Hawkes *et al.*, 2020) will hopefully provide the necessary information to wetland managers and other stakeholders, enabling a local appraisal of mosquito communities which the authors hope will further develop knowledge on this important group of Diptera, while supporting the important role of healthy wetlands in responding to a range of global climate and environmental challenges. However, the authors recognise that these assessments reflect findings from both the literature and the 12 wetland systems studied. It is likely that further field work at additional wetlands will provide new insights that can be used to enhance and modify these findings. However, based upon more than 14 years of mosquito surveillance data (unpublished) and previous in-depth studies of mosquitoes in English wetlands, the authors feel that this is a good assessment of the English mosquito fauna, with the caveat that unusual species, such as *Ae. vexans* (Vaux *et al.*, 2021) and *Cx. modestus* (Vaux *et al.*, 2015), which have focal distributions, are occasionally detected.

Finally, we ought to consider what impact this is likely to have on public health and the risk of disease transmission. The main five species reported from these wetlands (*Ae. caspius, Ae. detritus, Ae. cantans, Cq. richiardii, An. claviger*) are not currently linked in Europe as primary vectors of disease of public health concern. However there are various studies that have demonstrated naturally infected populations in the wild, or colonised populations have shown experimental laboratory infections, however this does not mean they are necessarily involved in disease transmission.

A number of viruses have been detected in wild-caught populations of *Ae. caspius*, however this does not necessarily confirm their vector role. It has been demonstrated as a competent vector of West Nile virus, via experimental transmission trials (Akhter *et al.*, 1982).

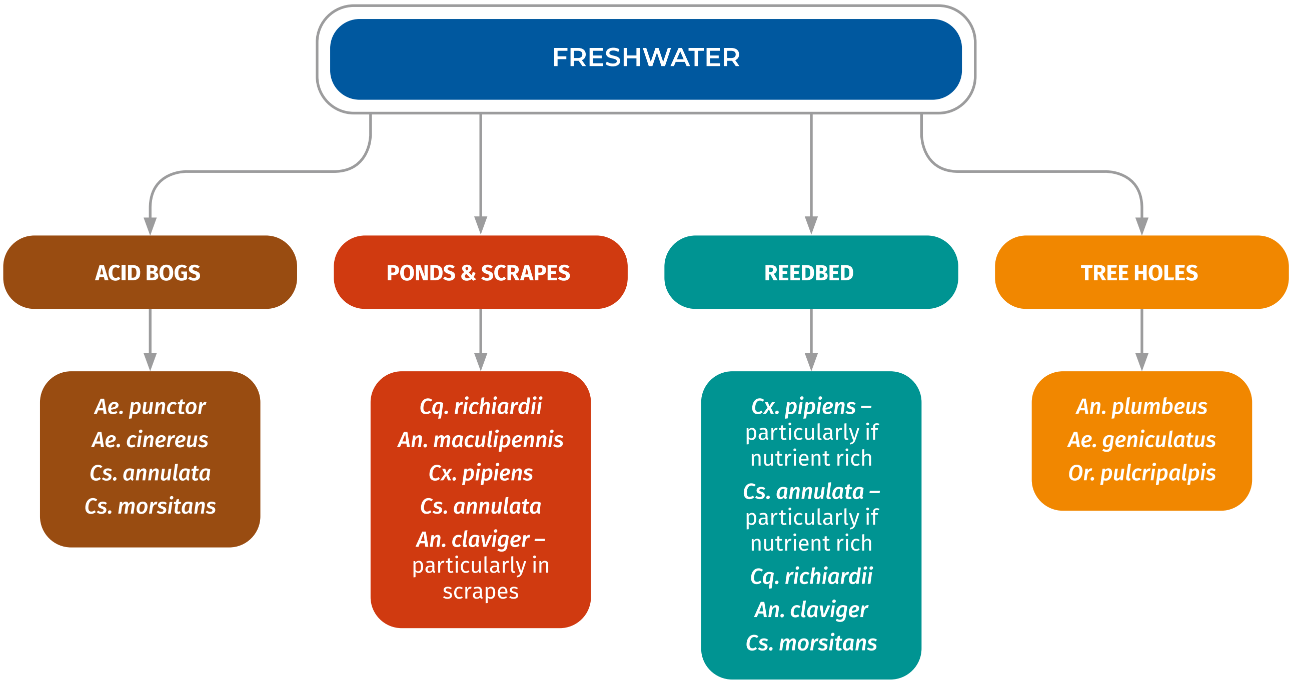

FIGURE 11 Mosquito prediction flow chart for acid bogs, ponds and scrapes, reedbed and tree holes. Adapted from Hawkes *et al.* (2020).

Rift Valley fever virus has been also detected in the salivary glands of field caught specimens after experimental infection (Moutailler *et al.*, 2008), and vector competence for RVFV has been demonstrated in experimental transmission studies (Turell *et al.*, 1996). Wild caught specimens have been experimentally infected with chikungunya virus, resulting in a 25% infection rate (Vazeille *et al.*, 2008), although they are not currently considered a vector in the field. Wild caught specimens have been found infected with a range of other pathogens, such as Tahyna virus (Calzolari *et al.*, 2010), Usutu virus (Mancini *et al.*, 2017) and *Dirofilaria immitis* (Latrofa *et al.*, 2012), but they are not considered primary vectors for these pathogens. In contrast it was found unable to experimentally transmit Zika virus (Nunez *et al.*, 2019).

Aedes detritus has been subjected to a number of experimental field trials, however this does not confirm vectorial capacity in the field. Vazeille *et al.* (2008), for example, infected wild-caught specimens with chikungunya virus, showing ~67% infection rate. Mackenzie-Impoinvil *et al.* (2015) provided evidence of experimental transmission of Japanese Encephalitis virus at 23–25 °C and Blagrove *et al.* (2016), using British wild-caught specimens, found no vector competence for either dengue nor chikungunya viruses, but they were laboratory competent for West Nile virus when maintained at 21 °C for 17 days.

Wild caught *Cq. richiardii* has been found infected with Batai, Tahyna (Aspock and Junz, 1968) and West Nile viruses (Szentpali-Gavaller *et al.*, 2014), *Dirofilaria repens* (Kemenesi *et al.*, 2015) and *Francisella tularensis* (Thelaus *et al.*, 2014). However, there is no clear evidence that they are primary vectors of any of these pathogens. Wild caught specimens of *Ae. cantans* have been found infected with West Nile virus (Labuda *et al.*, 1974) and Tahnya virus (Lundstrom, 1999).

Becker *et al.* (2010) considers *An. claviger* a malaria vector, as it was implicated in the historical transmission of *Plasmodium* (Collins and Jeffrey, 2007; Schaffner *et al.*, 2013), with some authors considering it still to be an important vector (Bueno Marí *et al.*, 2014). Historically it was implicated in malaria outbreaks in the 1950s/60s in the Eastern Mediterranean (Coluzzi *et al.*, 1964; Gramiccia, 1956), but currently there they are not implicated in European malaria transmission. As with the other species, a range of pathogens, such as Batai virus (Traavik *et al.*, 1985), Usutu virus (Becker *et al.*, 1984) and *F. tularensis* (Thelaus *et al.*, 2014) have been detected in wild-caught specimens, but this does not constitute vector risk. It has also been linked to possible role in the transmission of Myxoma virus (Service, 1971).

5 Conclusions

This paper presents data and discussion on the most common mosquito species in English wetlands, based on field studies at 12 wetlands across England. It also presents the empirical data underlying the decision trees presented in Hawkes *et al.* (2020). Mosquito trapping at English wetlands are dominated by five main species, and although none are currently involved in disease transmission in the UK, nor do they currently play significant roles in disease transmission in mainland Europe, it is prudent to continue to develop and manage wetlands so that they are resilient to future risk of disease transmission. Understanding which mosquito species are associated to different aquatic habitats, and the impact of their management, is critical to mitigate nuisance risk and in assessing risk for public health. Harnessing nature-based solutions to minimise mosquito-related issues has to be a key element of the sustainable management of current and future wetlands.

Supplementary material

Supplementary material can be found online at https://doi.org/10.6084/m9.figshare.25729665

Figure S1. Mosquitoes trapped at Alkborough, Lincolnshire.

Figure S2. Mosquitoes trapped at Arne, Poole harbour, Dorset.

Figure S3. Mosquitoes trapped at Bedford wetlands, Bedfordshire.

Figure S4. Mosquitoes trapped at Chippenham Fen, Cambridgeshire.

Figure S5. Mosquitoes trapped at Northward Hill, Kent.

Figure S6. Mosquitoes trapped at Shapwick Heath, Somerset Levels.

Figure S7. Mosquitoes trapped at Steart marshes, Somerset.

Figure S8. Mosquitoes trapped at Radipole Lake, Weymouth, Dorset.

Table S1. Total number of mosquitoes collected as larvae (per 3 litres of sampling water), recorded by species, location, visit month and wetland type.

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Conflict of interest

Jolyon Medlock is associate editor of the Journal of the European Mosquito Control Association; he had no influence in the review process and decision making on this manuscript. The other co-authors declare no conflict of interest.

Data availability

The detailed data that support the findings of this study is available on request.

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References

Abbott, A.J., 2018. The ecology of the mosquito *Culex modestus*, a potential vector of West Nile virus in the UK. PhD thesis, University of Greenwich, Greenwich, UK. Available at: https://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.777649)

Akhter, R. Hayes, C.G., Baqar, S. and Reisen, W.K., 1982. West Nile virus in Pakistan. III. Comparative vector capability of *Culex tritaeniorhynchus* and eight other species of mosquitoes. Transactions of the Royal Society of Tropical Medicine and Hygiene 76: 449–453. https://doi.org/10.1016/0035-9203(82)90132-8

Aspöck, H. and Kunz, C., 1968. Isolation of the Calovo-(= Batai-= Chitoor-)virus from *Anopheles* in Austria. Wiener Medizinische Wochenschrift 118: 497–498.

Bakonyi, T. and Haussig, J.M., 2020. West Nile virus keeps on moving up in Europe. Eurosurveillance 25: 2001938.

Becker, N., Petric, D., Zgomba, M., Boase, C., Dahl, C., Madon, M. and Kaiser, A., 2010. Mosquitoes and their control. Springer, New York, NY, USA.

Blagrove, M.S.C., Sherlock, K., Chapman, G.E., Impoinvil, D.E., McCall, P.J., Medlock, J.M., Lycett, G., Solomon, T. and Baylis, M., 2016. Evaluation of the vector competence of a native UK mosquito *Ochlerotatus detritus* (*Aedes detritus*) for dengue, chikungunya and West Nile viruses. Parasites and Vectors 9: 452. https://doi.org/10.1186/s13071-016-1739-3

Bueno Marí, R., Bernués Bañeres, A. and Jiménez Peydró, R., 2014. Biodiversity and larval habitat heterogeneity of mosquitoes (Diptera: Culicidae) in northern Spain. Acta Zoologica Bulgarica 66: 547–554.

Calzolari, M., Bonilauri, P., Bellini, R., Caimi, M., Defilippo, F., Maioli, G., Albieri, A., Medici, A., Veronesi, R., Pilani, R., Gelati, A., Angelini, P., Parco, V., Fabbi, M., Barbieri, I., Lelli, D., Lavazza, A., Cordioli, P. and Dottori, M., 2010. Arboviral survey of mosquitoes in two northern Italian regions in 2007 and 2008. Vector-Borne and Zoonotic Diseases 10: 875–884. https://doi.org/10.1089/vbz.2009.0176

Clarkson, M.J. and Enevoldson, T.P., 2020. The factors which influence the breeding and number of *Aedes detritus* in the Neston area of Cheshire, UK, the production of a local mosquito forecast and public bite reporting. Journal of European Mosquito Control Association 38: 17–32.

Cochet, A., Calba, C., Jourdain, F., Grard, G., Durand, G.A., Guinard, A., Noel, H., Paty, M-C. and Franke, F., 2022. Autochthonous dengue in mainland France, 2022: geographical extension and incidence increase. Eurosurveillance 27: 2200818.

Collins, W.E. and Jeffery, G.M., 2007. *Plasmodium malariae* : parasite and disease. Clinical Microbiology Reviews 20: 579–592. https://doi.org/10.1128/CMR.00027-07.

Coluzzi, M., Sacca, G. and Feliciangeli, D., 1964. The identity of *Anopheles claviger* populations in the Middle East. Rivista di Parassitologia 25: 123–128.

Committee on Climate Change 2020. Land use: policies for a net zero UK. Committee on Climate Change, London, UK.

Cranston, P.S., Ramsdale, C.D., Snow, K.R., and White, G.B., 1987. Keys to the adults, male hypopygia, fourth-instar larvae and pupae of British mosquitoes (Culicidae) with notes on their ecology and medical importance. Freshwater Biological Association Scientific Publication 48.

Department for Environment Food and Rural Affairs (DEFRA), 2022a. Landscape Recovery: more information on how the scheme will work. Defra Policy Paper, 6th January 2022.

Department for Environment Food and Rural Affairs (DEFRA), 2022b. Local Nature Recovery: more information on how the scheme will work. Defra Policy Paper, 6th January 2022.

European Centre for Disease Prevention and Control (ECDC), 2023. West Nile virus in Europe. ECDC, Stockholm, UK. Available at: https://www.ecdc.europa.eu/en/west-nile-virus-infection.

Folly, A.J., Lawson, B., Lean, F.Z., McCracken, F., Spiro, S., John, S.K., Heaver, J.P, Seilern-Moy, K., Masters, N., Hernández-Triana, L.M., Phipps, L.P., Nuñez, A., Fooks, A.R., Cunningham, A.A., Johnson, N. and McElhinney, L.M., 2020. Detection of Usutu virus infection in wild birds in the United Kingdom, 2020. Eurosurveillance 25: 2001732. https://doi.org/10.2807/1560-7917.ES.2020.25.41.2001732

Gearey, M., Church, A. and Ravenscroft, N., 2020. English Wetlands: Spaces of nature, culture, imagination. Palgrave Pivot, Cham, Switzerland. https://doi.org/10.1007/978-3-030-41306-4

Golding, N., Nunn, M.A., Medlock, J.M., Purse, B.V., Vaux, A.G. and Schäfer, S.M., 2012. West Nile virus vector *Culex modestus* established in southern England. Parasites and Vectors 5: 32. https://doi.org/10.1186/1756-3305-5-32

Gramiccia, G., 1956. *Anopheles claviger* in the Middle East. Bulletin of the World Health Organization 15: 816.

Hawkes, F.M., Medlock, J.M., Vaux, A.G.C., Cheke, R.A. and Gibson, G., 2020. Wetland mosquito survey handbook: assessing suitability of British wetlands for mosquitoes. Natural Resources Institute, Chatham, UK. Available at: http://wetlandlife.org/project-outputs

Hawkes, F.M., Acott, T.G. Basu Roy, S. Cheke, R.A. Church, A. Coates, P. Edwards, D. Ford, A. Gearey, M. Gibson, G. Graves, A. Lemke, H. Leslie, V.H. Medlock, J. Morris, J. Morrison, K. Ravenscroft, N. and Vaux, A.G.C., 2022. The wonder of wetlands: interdisciplinary investigations on the multiple values of English wetlands. University of Greenwich, Greenwich, UK.

Hayes, E.B. and Gubler, D.J., 2006. West Nile virus: epidemiology and clinical features of an emerging epidemic in the United States. Annual Review of Medicine 57: 181–194.

Intergovernmental Science-Policy Platform on biodiversity and Ecosystem Services (IPBES), 2017. Wetlands are critical to the success of the SDGs. IPBES Secretariat, 1st February 2017.

Kemenesi, G., Kurucz, K., Kepner, A., Dallos, B., Oldal, M., Herczeg, R., Vajdovics, P., Banyai, K. and Jakab, F., 2015. Circulation of *Dirofilaria repens*, *Setaria tundra*, and Onchocercidae species in Hungary during the period 2011–2013. Veterinary Parasitology 214: 108–113. https://doi.org/10.1016/j.vetpar.2015.09.010

Kirby, P., 2001. Habitat management for invertebrates: a practical handbook. Royal Society for Protection of Birds, Sandy, Bedfordshire, UK.

Kumar, R.,. McInnes, R.J., Everard, M., Gardner, R.C., Kulindwa, K.A.A. Wittmer, H. and Infante Mata, D., 2017. Integrating multiple wetland values into decision-making. Ramsar Policy Brief. Ramsar Convention Secretariat, Gland, Switzerland.

Labuda, M., Kozuch, O. and Gresikova, M., (1974) Isolation of West Nile virus from *Aedes cantans* mosquitoes in west Slovakia. Acta Virologica 18: 429–433.

Latrofa, M.S., Montarsi, F., Ciocchetta, S., Annoscia, G., Dantas-Torres, F., Ravagnan, S., Capelli, G. and Otranto, D., 2012. Molecular xenomonitoring of *Dirofilaria immitis* and *Dirofilaria repens* in mosquitoes from north-eastern Italy by real-time PCR coupled with melting curve analysis. Parasites and Vectors 5: 76. https://doi.org/10.1186/1756-3305-5-76

Lawson, B., Robinson, R.A., Briscoe, A.G., Cunningham, A.A., Fooks, A.R., Heaver, J.P, Hernández-Triana, L.M., John, S.K., Johnson, N., Johnston, C., Lean, F.Z.X., Macgregor, S.K., Masters, N.J., McCracken, F., McElhinney, L.M., Medlock, J.M., Pearce-Kelly, P., Seilern-Moy, K., Spiro, S., Vaux, A.G.C. and Folly, A.J., 2022. Combining host and vector data informs emergence and potential impact of an Usutu virus outbreak in UK wild birds. Scientific Reports 12: 10298. https://doi.org/10.1038/s41598-022-13258-2

Lundström, J., 1999. Mosquito-borne viruses in western Europe: a review. Journal of Vector Ecology 24: 1–39.

Lundström, J., Schäfer, M., Hesson, J. C., Blomgren, E., Lindstrom, A., Wahlqvist, P., Halling, A., Hagelin, A., Ahlm, C., Evander, M., Broman, T., Forsman, M. and Persson Vinnersten, T.Z., 2013. The geographic distribution of mosquito species in Sweden. Journal of the European Mosquito Control Association 31: 21–35.

Marshall, J.F., 1938. The British Mosquitoes. British Museum (Natural History), London, UK.

Mackenzie-Impoinvil, L., Impoinvil, D.E., Galbraith, S.E., Dillon, R.J., Ranson, H., Johnson, N., Fooks, A.R., Solomon, T. and Baylis, M., 2015. Evaluation of a temperate climate mosquito, *Ochlerotatus detritus* (= *Aedes detritus*), as a potential vector of Japanese encephalitis virus. Medical and Veterinary Entomology 29: 1–9.

Mancini, G., Montarsi, F., Calzolari, M., Capelli, G., Dottori, M., Ravagnan, S., Lelli, D., Chiari, M., Santilli, A., Quaglia, M., Federici, V., Monaco, F., Goffredo, M. and Savini, G., 2017. Mosquito species involved in the circulation of West Nile and Usutu viruses in Italy. Veterinaria Italiana 53: 97–110.

Medlock, J.M. and Snow, K.R., 2008. Natural predators and parasites of British mosquitoes. European Mosquito Bulletin 25: 1–11.

Medlock, J.M. and Leach, S.A., 2015. Effect of climate change on vector-borne disease risk in the UK. The Lancet Infectious Diseases 15: 721–730. https://doi.org/10.1016/S1473-3099(15)70091-5.

Medlock, J.M., Snow, K.R. and Leach, S., 2005. Potential transmission of West Nile virus in the British Isles: an ecological review of candidate mosquito bridge vectors. Medical and Veterinary Entomology 19: 2–21. https://doi.org/10.1111/j.0269-283X.2005.00547.x

Medlock, J.M., Hansford, K.M., Anderson, M., Mayho, R. and Snow, K.R., 2012. Mosquito nuisance and control in the UK − A questionnaire-based survey of local authorities. European Mosquito Bulletin 30: 15–29.

Medlock, J.M. and Vaux, A.G.C., 2011. Assessing the possible implications of wetland expansion and management on mosquitoes in Britain. European Mosquito Bulletin 29: 38–65.

Medlock, J.M. and Vaux, A.G.C., 2013. Colonization of UK coastal realignment sites by mosquitoes: implications for design, management, and public health. Journal of Vector Ecology 38: 53–62. https://doi.org/10.1111/j.1948-7134.2013.12008.x

Medlock, J.M. and Vaux, A.G.C., 2014. Colonization of a newly constructed urban wetland by mosquitoes in England: implications for nuisance and vector species. Journal of Vector Ecology 39: 249–260. https://doi.org/10.1111/jvec.12099

Medlock, J.M. and Vaux, A.G.C., 2015a. Seasonal dynamics and habitat specificity of mosquitoes in an English wetland: implications for UK wetland management and restoration. Journal of Vector Ecology 40: 90–106. https://doi.org/10.1111/jvec.12137

Medlock, J.M. and Vaux, A.G.C., 2015b. Impacts of the creation, expansion and management of English wetlands on mosquito presence and abundance – developing strategies for future disease mitigation. Parasites and Vectors 8: 142. https://doi.org/10.1186/s13071-015-0751-3

Medlock, J.M., Vaux, A.G.C., Cull, B., Schaffner, F., Gillingham, E., Pfluger, V. and Leach, S., 2017 Detection of the invasive mosquito species *Aedes albopictus* in southern England. Lancet Infectious Diseases 17: 140. https://doi.org/10.1016/S1473-3099(17)30024-5

Medlock, J.M., Hansford, K.M., Vaux, A.G.C., Cull, B., Gillingham, E. and Leach, S., 2018. Assessment of the public health threats posed by vector-borne disease in the United Kingdom (UK). International Journal of Environmental Research and Public Health 15: 2145. https://doi.org/10.3390/ijerph15102145

Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Synthesis, ed. MEA. Island Press, Washington, DC, USA.

Moutailler, S., Krida, G., Schaffner, F., Vazeille, M. and Failloux, A-B., 2008 Potential vectors of Rift Valley fever virus in the Mediterranean region. Vector-Borne and Zoonotic Diseases 8: 749–754. https://doi.org/10.1089/vbz.2008.0009

Núñez, A.I., Talavera, S., Aranda, C., Birnberg, L., Rivas, R., Pujol, N., Verdun, M., Failloux A-B. and Busquets, N., 2019. European *Aedes caspius* mosquitoes are experimentally unable to transmit Zika virus. Parasites and Vectors 12: 363. https://doi.org/10.1186/s13071-019-3620-7

Pires, C.A., Ribeiro, H., Capela, R.A. and Ramos, H.C., 1982. Research on the mosquitoes of Portugal (Diptera, Culicidae) VI – The mosquitoes of Alentejo. Anais do Instituto de Higiene e Medicina Tropical 8: 79–102.

Ramsdale, C.D. and Snow, K.R., 1995. Mosquito control in the UK. Dagenham, University of East London, London, UK.

Rezza, G., 2018. Chikungunya is back in Italy: 2007–2017. Journal of Travel Medicine 25: 1–4 https://doi.org/10.1093/jtm/tay004

Rudolf, I., Šikutová, S., Šebesta, O., Mendel, J., Malenovský, I., Kampen, H., Medlock, J. and Schaffner, F., 2020. Overwintering of *Culex modestus* and other mosquito species in a reedbed ecosystem, including arbovirus findings. Journal of the American Mosquito Control Association 36: 257–260. https://doi.org/10.2987/20-6949.1

Schäfer, M. L., Lundström, J. O., Pfeffer, M., Lundkvist, E. and Landin, J., 2004. Biological diversity versus risk for mosquito nuisance and disease transmission in constructed wetlands in southern Sweden. Medical and Veterinary Entomology 18: 256–267. https://doi.org/10.1111/j.0269-283X.2004.00504.x

Schaffner, F., Marquine, M., Pasteur, N. and Raymond, M., 2003. Genetic differentiation of *Anopheles claviger s.s.* in Europe. Journal of Medical Entomology 40: 865–875

Schaffner, F., Medlock, J.M. and Van Bortel, W., 2013. Public health significance of invasive mosquitoes in Europe. Clinical Microbiology and Infection 19: 685–692. https://doi.org/10.1111/1469-0691.12189

Service, M.W., 1968. Observations on feeding and oviposition in some British mosquitoes. Entomologia Experimentalis et Applicata 11: 286–290.

Service, M.W., 1969. Observations on the ecology of some British mosquitoes. Bulletin of Entomological Research 59: 161–164.

Service, M.W., 1971. Feeding behaviour and host preferences of British mosquitoes. Bulletin of Entomological Research 60: 653–661.

Service, M.W., 1973. The biology of *Anopheles claviger* (Mg.) (Diptera, Culicidae) in southern England. Bulletin of Entomological Research 63: 347–359.

Service, M.W., 1971. A reappraisal of the role of mosquitoes in the transmission of myzomatosis in Britain. Journal of Hygiene 69: 105–111

Service, M.W., 1994. The biology of *Culiseta morsitans* and *Culiseta litorea* in England. Bulletin of Entomological Research 84: 97–104.

Service, M.W. and Smith, G., 1972. Notes on the biology of *Aedes flavescens* (Muller) (Diptera, Culicidae) in England. Entomologist's Monthly Magazine 108: 35–37.

Snow, K.R., 1990. Mosquitoes. Naturalists' Handbook 14. Richmond Publishing Co. Ltd, Slough, UK.

Szentpáli-Gavallér, K., Antal, L., Toth, M., Kemenesi, G., Soltesz, Z., Dan, A., Erdelyi, K., Banyai, K., Balint, A., Jakab, F. and Bakonyi, T., 2014. Monitoring of West Nile virus in mosquitoes between 2011–2012 in Hungary. Vector-Borne and Zoonotic Diseases 14: 648–655. https://doi.org/10.1089/vbz.2013.1549

Thelaus, J., Andersson, A., Broman, T., Backman, S., Granberg, M., Karlsson, L., Kuoppa, K., Larsson, E., Lundmark, E., Lundstrom, J.O., Mathisen, P., Naslund, J., Schafer, M., Wahab, T. and Forsman, M., 2014. *Francisella tularensis* subspecies *holarctica* occurs in Swedish mosquitoes, persists through the developmental stages of lboratory-infected mosquitoes and is transmissible during blood feeding. Microbial Ecology 67: 96–107. https://doi.org/10.1007/s00248-013-0285-1

Traavik, T., Mehl, R. and Wiger, R., 1985. Mosquito-borne arboviruses in Norway: further isolations and detection of antibodies to California encephalitis viruses in human, sheep and wildlife sera. Journal of Hygiene 94: 111–122. https://doi.org/10.1017/S0022172400061180

Vlaskamp, D.R., Thijsen, S.F., Reimerink, J., Hilkens, P., Bouvy, W.H., Bantjes, S.E., Vlaminckx, B.J., Zaaijer, H., van den Kerkhof, H.H., Raven, S.F. and Reusken, C.B., 2020. First autochthonous human West Nile virus infections in the Netherlands, July to August 2020. Eurosurveillance 25: 2001904. https://doi.org/10.2807/1560-7917.ES.2020.25.46.2001904

Vaux, A.G.C., Gibson, G.I., Hernandez-Triana, L., Cheke, R.A., McCracken, F., Jeffries, C.L., Horton, D.L., Springate, S., Johnson, N., Fooks, A., Leach, S. and Medlock, J.M., 2015. Enhanced West Nile virus surveillance in the North Kent marshes, UK. Parasites and Vectors 8: 91. https://doi.org/10.1186/s13071-015-0705-9.

Vaux, A.G.C., Dallimore, T. Cull, B., Schaffner, F., Strode, C., Pflüger, V., Murchie, A.K., Rea, I., Newham, Z., McGinley, L., Catton, M., Gillingham E.L. and Medlock, J.M., 2019. The challenge of invasive mosquito vectors in the U.K. during 2016–2018: a summary of the surveillance and control of *Aedes albopictus*. Medical and Veterinary Entomology 33: 443–452. https://doi.org/10.1111/mve.12396

Vaux, A.G.C., Johnston, C., Dallimore, T., McGinley, L., Strode, C., Murchie, A.K., Iyanger, N., Pudney, R., Chow, Y., Brand, M., Rea, I. and Medlock, J.M., 2020. Working towards a co-ordinated approach to invasive mosquito detection, response and control in the UK. International Journal of Environmental Research and Public Health 17: 5166. https://doi.org/10.3390/ijerph17145166

Vaux, A.G.C., Watts, D., Findlay-Wilson, S., Johnston, C., Dallimore, T., Drage, P. and Medlock, J.M., 2021. Identification, surveillance and management of *Aedes vexans* in a flooded river valley in Nottinghamshire. Journal of the European Mosquito Control Association 39: 15–25. https://doi.org/10.52004/JEMCA2021.0001

Vazeille, M., Jeannin, C., Martin, E., Schaffner, F. and Failloux, A-B., 2008. Chikungunya: A risk for Mediterranean countries? Acta Tropica 105: 200–202. https://doi.org/10.1016/j.actatropica.2007.09.009

Welch, M.D., 2021 An inland occurrence of the West Nile virus vector *Culex modestus* Ficalbi (Diptera, Culicidae) in Ely, Cambridgeshire, UK. Dipterists Digest.

Wilder-Smith, A., Quam, M., Sessions, O., Rocklov, J., Liu-Helmersson, J., Franco, L. and Khan, K.. 2014. The 2012 dengue outbreak in Madeira: exploring the origins. Eurosurveillance 19: 20718.

World Health Organization (WHO), 2022. The history of Zika virus. Available at: https://www.who.int/news-room/feature-stories/detail/the-history-of-zika-virus.

Ziegler, U., Lühken, R., Keller, M., Cadar, D., van der Grinten, E., Michel, F., Albrecht, K., Eiden, M., Rinder, M., Lachmann, L., Höper, D., Vina-Rodriguez, A., Gaede, W., Pohl, A., Schmidt-Chanasit, J. and Groschup, M.H., 2019. West Nile virus epizootic in Germany, 2018. Antiviral Research 162: 39–43.