European Mosquito Bulletin, 25 (2008), 1-11.
Journal of the European Mosquito Control Association
ISSN1460-6127; www.europeanmosquitobulletin.com
First published online 30 April 2008

Natural predators and parasites of British mosquitoes – a review

J.M. Medlock[1] and K.R. Snow[2]
[1]Health Protection Agency, Porton Down, Salisbury, Wiltshire, U.K. Email: jolyon.medlock@hpa.org.uk.
[2]School of Health and Bioscience, University of East London, London, U.K. Email: snow373@btinternet.com

Abstract
This paper reviews the recorded predators of all life stages of British mosquitoes and assesses their relative effectiveness in limiting mosquito populations. Predators vary markedly in the different habitats that immature and adult mosquitoes frequent, with representatives from at least six insect orders, thirteen arachnid families, as well as crustaceans, amphibians, fish, birds and mammals. We conclude that predators and parasites have a limited but significant effect on overall mosquito populations, and their role should be considered when implementing habitat management, mosquito control and when modeling mosquito population dynamics.

Keywords: mosquito, predator, parasite, British

Introduction

Increasing biodiversity through the conservation of natural habitats, increasing wetland and saltmarsh areas, together with the preservation of water for eco-friendly gardening, all potentially increase the available aquatic sites for mosquitoes endemic to the British Isles. Despite their obvious nuisance, mosquitoes are part of our natural fauna, occupying a variety of niches, with each species contributing to a complex food web. Larval mosquitoes filter a variety of submerged or floating food particles and graze on a range of algae, leaf detritus and animal remains. As adults, the females procure a blood-meal (from humans, livestock, birds, reptiles and mammals, depending on the species) and supplement their diet with plant juices. The males do not blood-feed, relying solely on plant juices.

Throughout their lifecycle mosquitoes are exposed to a wide range of predators as eggs, larvae and pupae, and as imagines during emergence and oviposition, at rest in vegetation, whilst flying or swarming, and during overwintering. The range of predators varies in the different habitats that mosquitoes occupy, with representatives from at least six insect orders, thirteen families of arachnids, as well as crustaceans, amphibians, fish, birds and mammals. While these predators may have limited effect on eradicating populations of mosquitoes, the role of mosquitoes as a prey species is an important consideration for those employed in wildlife conservation, habitat management and mosquito control.

It is difficult to assess the direct effect of all possible predators on mosquito populations, and it is unlikely that any list will be definitive. This article reviews all available entomological literature and unpublished observations of the authors on the predators and parasites of British mosquitoes, detailing the predators recorded at each life stage and within each of the main five aquatic habitats in UK.

Predators of mosquito eggs

Few studies have considered the predators of eggs of British mosquitoes. The potential invertebrate egg predators in and around *Ochlerotatus cantans* (Meigen) oviposition sites in woodlands near Monks wood in Huntingdonshire were investigated by Service (1973a, 1977). Precipitin tests on gut smears were carried out on a sample of 260 Acari [mites] (including 104 *Macrocheles* spp., 89 *Peragamasus* spp. and 67 *Gepholapsis* spp.), 294 Coleoptera [beetles] (including 7 Carabidae [ground beetles], 26 Dytiscidae [predacious diving beetles], 35 Hydrophilidae [water scavenger beetles], 4 Scydmaenidae [ant-like stone beetles], 183 Staphylinidae [rove beetles], 11 Cryptophagidae [silken fungus beetles], 21 Lathridiidae [minute brown scavenger beetles] and 7 Anthicidae [ant-like flower beetles]), 19 Chilopoda [centipedes] and 11

Lumbricidae [earthworms], however none of the precipitin tests gave a positive result. Service commented that the likelihood of identifying a positive meal from an egg predator is much less than for a larval predator, and that to achieve a positive result, the gut smear of any potential predator would have to be made soon after predation and therefore the possibility of confirming predation by the precipitin test method may be limited. Nevertheless, despite the lack of published quantifiable evidence, predation by fish and certain invertebrates on eggs that have been deposited on the water surface (such as in *Culex* spp., *Anopheles* spp. and certain *Culiseta* spp.) is likely to have an impact on numbers.

Predators of mosquito larvae and pupae

The predators of mosquito larvae and pupae are likely to vary depending upon the aquatic habitat occupied by the mosquito, and these habitats can be separated crudely into five categories: (a) permanent freshwater, (b) temporary woodland pools/flooded habitats, (c) brackish water salt-marshes, (d) artificial container habitats and (e) tree holes.

Permanent freshwater immature sites

Three separate studies have investigated the predators of mosquito larvae and pupae in permanent freshwater habitats in Great Britain. In studies at two permanent freshwater ponds at Silwood Park in Berkshire by Onyeka (1983), evidence of predation, by positive gut smears, on *Culex pipiens s.l.* Linnaeus and *Culex torrentium* Martini was reported in three insect orders: Odonata [dragonflies and damselflies], Coleoptera and Hemiptera [true bugs], and by amphibians [newts]. This work was later supported by observation of the predators of *Anopheles claviger* (Meigen) from ponds in East Lothian by Jeffries (1988) who placed ten 2nd and 3rd instar larvae in weed-filled beakers and recorded the number of larvae consumed by a number of different invertebrate predators within 24 hours. The third study by Snow (unpublished) assessed the propensity for freshwater fish from ponds in Epping Forest in Essex to ingest larvae of *Ochlerotatus punctor* (Kirby) and *Cx. pipiens s.l.*, with some evidence of predation of larvae by certain Odonata.

Regarding Odonata, Onyeka (1983) found high predation rates in anisopteran [dragonflies] nymphs, with positive gut smears reported from 58/94 *Sympetrum striolatum* [common darter] and 40/77 *Libellula depressa* [broad-bodied chaser], and in zygopteran [damselflies] nymphs, with evidence of predation in 54/84 *Coenagrion puella* [azure damselfly], 25/73 *Coenagrion mercuriale* [southern damselfly], 28/56 *Ischnura elegans* [blue-tailed damselfly] and 31/60 *Pyrrhosoma nymphula* [large red damselfly]. In addition Jeffries (1988) also reported predation of *An. claviger* larvae by *Enallagma cyathigerum* [common blue damselfly] which had consumed 1 of 10 larvae within 24 hours. Nymphs of three dragonfly species were observed by Snow (unpublished) feeding on larvae of *Oc. cantans/punctor* in ponds in Epping Forest: *Anax imperator* [emperor dragonfly], *L. depressa* and *S. striolatum*. It is likely that other species of Odonata act as larval predators, as more than 50% of Odonata surveyed by Onyeka had preyed on larvae, with mosquito larvae likely to be an important part of their diet.

Adult and larval beetles from two families, Dytiscidae and Halipidae [crawling water beetles], were tested by Onyeka (1983) with representatives from each found to have preyed on mosquito larvae. Dytiscid predators included adult and larval *Agabus bipustulatus* (3/23 and 23/46 respectively), adult and larval *Dytiscus marginalis* [great diving beetle] (7/30 and 19/50 respectively), larval *Colymbetes fuscus* (13/22), adult and larval *Hydroporus* sp. (2/5 and 1/8 respectively – however no *H. memnonius* were positive, n=2), adult *Hyphydrus ovatus* (8/24), larval *Rhantus* sp. (1/1) and *Hygrotus* sp. (1/6, no stage given). Only one halipid beetle was surveyed and found to be a predator: larval *Peltodytes* sp. (3/20). Jeffries (1988) confirmed predation by *A. bipustulatus* and *D. marginalis* (2/10 and 1/10 *An. claviger* larvae consumed respectively), however there was no evidence of predation by *Hydroporus palustris* or *Hydroporus erythrocephalus*.

Representatives from two families of Hemiptera were also tested by Onyeka (1983): in Gerridae, 2/15 *Gerris gibbifer* [pondskater] and 1/15 *Gerris lacustris* [pondskater] had preyed on *Culex* species, however in Notonectidae, there was no evidence of predation in 16 *Notonecta glauca* [water boatman]. Jeffries (1988), in contrast, did find evidence of predation by *N. glauca* (consuming 1/10 *An. claviger* larvae) as well as a high predatory instinct (all ten larvae

European Mosquito Bulletin, 25 (2008), 1-11.
Journal of the European Mosquito Control Association
ISSN1460-6127; www.europeanmosquitobulletin.com
First published online 30 April 2008

consumed) in the corixid bug *Cymatia bonsdorfii* [water bug]. Jeffries reported no evidence of predation by *Polycelis tenuis* (Turbellaria: Tricladida) [land flatworms] or *Chaoborus crystallinus* [phantom midge] (Diptera).

Fish species	***Ochlerotatus punctor***	***Culex pipiens***
Bleak *Alburnus alburnus*	+++	+++
Carp *Cyprinus carpio*	+	+
Crucian carp *Carassius carassius*	+	
Goldfish *Carassius auratus*	+++	+++
Gudgeon *Gobio gobi*	++	+
Minnow *Phoxinus phoxinus*	+++	+++
Perch *Perca fluviatilis*	++	++
Roach *Rutilus rutilus*	++	++
Rudd *Scardinius erythrophthalmus*	++	+++
Stickleback *Gasterosteus aculeatus*	+++	+++
Tench *Tinca tinca*	+	

Table 1. Freshwater fish ingesting mosquito larvae. The number of symbols shows the number of larvae ingested by 3 fish each offered 20 larvae of either *Ochlerotatus punctor or Culex pipiens* for 30 minutes (+++ 41-60 larvae; ++ 21-40 larvae; + 1-20 larvae). The absence of a symbol indicates that no larvae were eaten.

Regarding amphibians, gut smears of *Trituris vulgaris* [smooth newt] tested by Onyeka showed high levels of predation (30/40), and although there is no available quantitative data for other species, Snow (unpublished) observed predation of mosquito larvae (and resting adults) in Epping Forest, Essex by *Trituris cristatus* [great crested newt], *T. vulgaris*, *Rana temporaria* [common frog] and *Bufo bufo* [common toad]. Ramsdale & Snow (1995) also listed tadpoles as predators of mosquito larvae and it is likely that all feeding stages of amphibians are important predators in a number of permanent and semi-permanent aquatic habitats.

Fish are important predators of mosquito larvae and are frequently used in biological control programmes, indeed Jenkins (1964) listed 226 vertebrate predators of mosquito larvae and 22 of mosquito adults, of which 190 were fish. Snow (unpublished) tested the propensity for twelve species of freshwater fish (all measuring under 6 inches in length) from Epping Forest to feed on mosquito larvae in the laboratory, each in a 120 x 60 x 60 cm glass aquarium. They were allowed to acclimatize in their surroundings without the addition of food for 48 hours and then 4th instar larvae of either *Oc. punctor* (*Op*) or *Cx. pipiens* (*Cp*) were introduced. In each observation, 20 larvae were placed in the tank, and three specimens of each species of fish were observed for 30 minutes. The combined results are shown above in Table 1.

Snow concluded that the most voracious mosquito larvae feeders were *Phoxinus phoxinus*, *Alburnus alburnus*, *Carassius auratus* and. *Gasterosteus aculeatus*. According to Ramsdale & Snow (1995), European predaceous fish include *Cyprinus carpio, Tinca tinca, G. aculeatus*, and, in Hayling Island, *Gobius microps* [Goby]. *Scardinius erythrophthalmus* were also introduced into ponds to keep down mosquitoes on Ministry of Defence land on the Isle of Grain just prior to the 1939-45 war (Ramsdale & Snow, 1995).

Temporary freshwater pools and flooded immature habitats

Several species of *Aedes and Ochlerotatus*, particularly *Oc. cantans* and *Oc. punctor,* use temporary freshwater pools and flooded habitats as larval habitats. Service (1973a; 1977) and Snow (unpublished) conducted studies on predation of *Oc. cantans and Oc. punctor* in temporary pools and small ponds in Monks wood and Ham Street woods in Kent, and in Epping Forest, Essex, respectively.

Gut smears of potential predators of *Oc. cantans* larvae were tested by Service (1973a, 1977) from various insect orders: Trichoptera [caddis flies], Coleoptera, Hemiptera, Plecoptera [stoneflies], Ephemeroptera [mayflies], and various other invertebrate groups: Tricladida, Isopoda [slaters], and Amphipoda [shrimps]. Snow (unpublished) also observed predation of *Oc. cantans/punctor* larvae by various Coleoptera, Hemiptera and Odonata.

Caddisfly larvae were common arthropods associated with *Oc. cantans* aquatic sites in the Monks wood study ditch, however only a small percentage of larval gut smears of *Trichostegia minor* (3/230) and *Glyphotaelius pellucides* (2/175) were positive. However, when Service placed caddisfly larvae in tanks in the laboratory with *Oc. cantans* larvae, there was no evidence of predation except when larvae were injured or confined to small amounts of water, concluding that these species of caddisfly are probably not predators but capable of scavenging on injured larvae as benthic feeders. Furthermore, caddisfly species from Phryganidae [giant casemakers] (12 larval *Limnophilus* sp.) and Leptocercidae [long-horned caddisfly] (3 larval *Leptocercus* sp.) were negative when tested.

According to the gut smear analysis, a large proportion of dytiscid beetles were also reported to have preyed on *Oc. cantans* larvae by Service (1973a, 1977). Particular species that showed evidence of predation were adult and larval *Agabus bipustulatus* (4/57 and 19/34), larval *Dytiscus semisulcatus* (2/8) and larval *Agabus sturmii* (1/1). Predation of larval *Oc. cantans/punctor* by adult *Dytiscus marginalis* was also observed by Snow, as was predation by adult *Gyrinus natator* [whirligig beetle]. Service (1977) also reported that a further 56/140 unidentified dytiscid beetles had also preyed on *Oc. cantans* larvae, confirming the predatory role of dytiscids in such habitats. A number of experiments were conducted by Service (1973a) in the laboratory on the predatory behaviour of *A. bipustulatus*, and in 29 laboratory trials with 3rd instar *A. bipustulatus*, mean values of 4.4 2nd instar, 3.2 4th instar and 0.8 pupal *Oc. cantans* were consumed within 24 hours, with means of 1.5 (2nd), 1.9 (4th) and 0.7 (pupae) eaten in 24 hours by 2nd instar *A. bipustulatus*. Although there was a high incidence rate of feeding on *Oc. cantans* larvae by dytiscid larvae, Service (1973a, 1977) did not consider them to cause any appreciable reduction of the immature stages of *Oc. cantans*, which Service attributed to the low density of beetle larvae. The reduced predation on pupae was explained by the beetle's tendency to remain on the bottom of the pool, where they do not encounter pupae that tend to remain at the water surface for considerably longer periods.

Other beetle species, including other members of Dytiscidae, as well as Hydrophilidae and Helodidae [marsh beetles] were also sampled by Service (1977) with all gut smears negative for *Oc. cantans*. In Dytiscidae these included: 5 adult *Hygrotus inequalis*, 4 adult *Hydroporus planus*, 2 adult *H. palustris*, 2 adult *H. tesellatus*, 4 adult *H. pubescens*, 20 adult *H. memnonius*, 8 adult *H. angustatus*, 6 adult *H. gyllenhalii,* 2 adult *H. erythocephalus,* 2 adult *Hyphydrus ovatus*, 2 larval *Agabus chalconotus*, 4 adult *A. sturmii*, 1 adult *A. ungunicularis*, 2 adult *Laccophilus minutus*, 3 adult *Ilybius fenestratus* and 3 adult *Dytiscus semisulcatus*. Hydrophilid beetles included 4 adult *Helophorus grandis* and 3 adult *Anacaena limbata*; and 86 unspecified helodid beetles.

With reference to Hemiptera, Service (1973) found some evidence of predation in gut smears of the pondskaters *Gerris lacustris* (3/34) and *Gerris gibbifer* (1/13), but not by 2 adult *Hydrometra stagnorum* [water measurer] (Hemiptera: Hydrometridae). Snow (unpublished) confirmed predation of larval *Oc. cantans/punctor* by adult *Gerris lacustris* by direct observation, with evidence also of predation by adult *Nepa cinerea* [water scorpion], adult *Notonecta glauca* [backswimmer], adult *Velia caprai* [water cricket], adult *Corixa punctata* [water boatman] and adult *H. stagnorum*. The latter are known for walking quite slowly on the surface of still or slow-moving water and spearing their prey through the surface film of water, sucking out the larva's body contents with their long mouthparts.

Other invertebrates surveyed by Service (1977) included large numbers of isopod (106 adult *Asellus aquaticus*) and amphipod (78 adult *Gammarus pulex*) crustaceans, as well as mayflies (60 nymphal *Cloeon dipterum*) and stoneflies (109 nymphal *Nemoura cinerea*), but all gut smears were negative for predation on *Oc. cantans.* Interestingly though,

European Mosquito Bulletin, 25 (2008), 1-11.
Journal of the European Mosquito Control Association
ISSN1460-6127; www.europeanmosquitobulletin.com
First published online 30 April 2008

Service found evidence of predation in 2/34 land flatworms (unidentified Tricladida) surveyed.

Brackish water salt-marsh habitat

The brackish water aquatic habitats adopted by some of our coastal species exposes mosquitoes to a range of different brackish-water tolerant invertebrates. The role of *Gammarus duebeni* [brackish-water amphipod] as a predator of the salt-marsh mosquito *Ochlerotatus detritus* (Haliday) was investigated in the estuary of the River Test and on Hayling Island, both in Hampshire, by Lockwood (1986) and Roberts (1995) respectively, and around Sandwich, Kent by Molenkamp (1998). Additionally Roberts also studied the predatory nature of *Palaemonetes varians* [prawn/grass shrimp/ditch shrimp] on *Oc. detritus* at Hayling, and Molenkamp studied predation by *Sphaeroma rugicauda* [estuarine isopod] and *Orchestia cavimana* [talitrid amphipod] on *Oc. detritus* at Sandwich/Pegwell bay. All three studies found that *G. duebeni* was an efficient predator of mosquito larvae: Lockwood (1986) found that of 30 *Ochlerotatus* larvae left in a tank with 10 male and 6 female *Gammarus*, only 18 had survived after 24 hours, and only 8 after 64 hours, and Roberts (1995) found that a mature gammarid could consume 4-8 larvae in 24 hours. Molenkamp (1998) carried out extensive studies on predation by *G. duebeni* and showed that the rate that they consumed larvae was not affected by providing a choice of food (e.g. mud containing other potential prey species). Consumption rates in one study showed that almost all of ~150 larvae were consumed within 8 days, at a rate of 13-18 larvae per gammarid, and 1.6-2.3 larvae/gammarid/day. Lockwood (1986) showed that their ability to prey upon *Oc. detritus* larvae was not affected by changing salinities and that feeding on mosquito larvae was more a result of chance encounter, with no evidence of *G. duebeni* changing direction to specifically target mosquito larvae. In fact larvae were frequently seen escaping from an attack by *G. duebeni*. *Gammarus duebeni* is undoubtedly an efficient predator of saltmarsh mosquito larvae, active throughout the year and able to tolerate periods of drought. Although mosquito larvae perhaps form some part of the omnivorous diet of *G. duebeni*, Roberts (1995) considered that the voracious feeding of *P. varians* in comparison was quite apparent. Roberts (1995) reported that *P. varians* could consume 22-30 larvae per hour, and where there was a surfeit of mosquito larvae, the shrimps would continue killing larvae, sometimes dropping them half eaten. Molenkamp (1998) also reported low levels of predation by the amphipod *O. cavimana* (4/66 after 2 days, 23/66 after 6 days), however the isopod *S. rugicauda* consumed no larvae even after 25 days. It appears therefore that brackish-water amphipods are important predators of salt-marsh mosquitoes.

Artificial container habitats

In addition to the studies at freshwater ponds at Silwood Park, Onyeka (1983) also studied the predators of *Cx. pipiens* and *Cx. torrentium* larvae breeding in artificial container habitats. Although the fauna of such an aquatic site would be expected to be less diverse than a natural permanent water site, good numbers of Coleoptera were recorded, with a similar assemblage of dytiscid and hydrophilid predators. High incidences of predation were again reported in gut smears of larval and adult *Agabus bipustulatus* (55/75 and 8/22 respectively) and larval and adult *Dytiscus marginalis* (38/67 and 6/16). These predatory rates are higher than in permanent freshwater sites, as would be expected due to the reduced size of container habitats affording less protection or escape routes from larval beetles. Other dytiscid predators included 7/11 adult *Hydroporus memnonius*, 4/7 larval and 3/12 adult *Hydroporus* sp. and 1/4 adult *Hyphydrus ovatus* – all of which had not preyed on larvae in permanent freshwater sites. The only hydrophilid beetle surveyed and found to have fed on *Culex* spp. was the larva of *Helophorus aquaticus* (3/13).

Tree holes

Several papers: Beattie & Howland (1929) in Burnham Beeches, Bucks; Kitching (1971) in Wytham wood, Oxfordshire; and Yates (1979) at Monks wood, detail the ecology of tree-holes and their associated invertebrate fauna, with some mention of the possible predators of dendrolimnic mosquitoes, such as *Anopheles plumbeus* Stephens and *Aedes geniculatus* (Olivier). Beattie & Howland (1929) reported insects associated with tree-hole mosquitoes in beech trees as *Metriocneumus martini* (chironomid [tree-hole midge] larvae), *Phaonia* *mirabilis* (anthomyiid larvae), *Myiatropa florea* (syrphid [hover fly] larvae) and *Helodes* sp. (Coleoptera). Kitching (1971) also reported *M. martini*, describing it as a largely indiscriminate saprophage which from time to time feeds selectively on dead animal remains. Its role as a predator is non-existent or, at most, very exceptional. Kitching (1971) also reported the presence of saprophagous *M. florea* hoverflies, again considered unlikely to prey on mosquito larvae. Additional invertebrate tree-hole fauna reported by Kitching (1971) included *Dasyhelea dufouri* (Ceratopogonidae), a plant and detritus feeder, and *Prionocyphon serricornis* (Coleoptera) − also saprophagous. Yates (1979), studying the possible predators of *Ae. geniculatus*, again reported the larvae of *P. serricornis* and considered them saprophagous, and that an omnivorous fully grown larva of the caddisfly *Glyphotaelius pellucides* (Trichoptera) only contained leaf litter in its gut. It appears therefore that no invertebrates prey on mosquito larvae and pupae in tree holes, however various other invertebrates (e.g. arachnids) associated with tree holes have been reported to prey on emerging or ovipositing adults, and these are discussed below.

Predators of emerging adults

The predators of adults emerging from temporary flooded habitats at Monks wood and Ham Street wood were reported by Service (1973a), from temporary pools/small ponds in Epping Forest by Snow (unpublished), from artificial containers and permanent freshwater ponds at Silwood Park by Onyeka (1983), and from tree-holes at Monks wood by Yates (1979). The most significant predators were predacious Diptera, primarily the Empididae [dance flies], Dolichopodidae [thick-headed flies] and to a lesser extent the Scatophagidae [dung flies] and Anthomyiidae. Representatives of various families of arachnid were also reported.

In April, coinciding with the emergence of *Oc. cantans* at Monks wood and Ham Street wood, Service (1973a) noted a large number of predacious flies, predominantly Empididae, that appeared to fly over and also settle on the water in the study ditch. They were occasionally seen to prey on both emerging adults and those that had completed emergence and were resting on the water. Service (1973a) collected 315 gut smears from six species of fly, and identified five species as potential predators. Three species were common, namely *Hilara interstincta* (54/162), *Hilara lugubris* (23/79) and *Rhamphomyia crassirostris* (17/84). The other two species were *Hilara pilosa* (9/33) and *Hilara cornicula* (1/1). Evidence of predation by *H. interstincta* (2/7) on emerging *Culex* spp. was also reported by Onyeka (1983) at ponds at Silwood Park, and on emerging *Oc. cantans/punctor* by Snow (unpublished) in Epping Forest.

Service (1973a) concluded that owing to the relatively large populations of these flies and their relatively high incidence of feeding on emerging *Oc. cantans* (and possibly ovipositing females), they probably caused a greater population loss than any predation on the immature stages. Service (1973a) estimated the total numbers of *Oc. cantans* emerging from the ditch in Monks wood in 1971 and 1972 as ~47,000 and ~28,000 respectively, and from several estimates made of predacious flies the average number on any one day in 1971 and 1972 during emergence was ~545 and ~382. Incorporating these data with the proportion having fed on emerging adult *Oc. cantans* (27.6%), and assuming they fed on one adult a day, a crude estimate of the numbers of mosquitoes eaten during the total emergence period was calculated. This period of adult emergence lasted 42 days in 1971 and 36 days in 1972 (Service, 1973a), and the total reduction in emerging adult numbers over this period was 6318 (13.4%) for 1971 and 3796 (13.6%) for 1972. This supported the conclusion that predation on emerging adults by Empididae was one of the most significant causes for mosquito predation.

A few species of other predacious Diptera were collected by Service (1973a), with evidence in gut smears of predation on *Oc. cantans* recorded in Dolichopodidae: 1/7 *Hercostomus* spp., 1/14 *Campsicnemus survipes* and 1/3 *Campsicnemus scambus*; Scatophagidiae: 1/4 *Scatophaga squalida*, and Anthomyiidae: 1/8 *Hydrophoria ruralis*. Snow (unpublished) additionally observed predation on *Oc. cantans/punctor* by the adult dolichopodidae *Poecilobothrus nobilitatus* and *Dolichopus popularis,* and by the adult dragonflies *Anax imperator* and *Sympetrum striolatum*. Onyeka (1983) also sampled 10 *Asilus* spp. (Asilidae [robber flies]) from freshwater ponds, with no evidence of predation.

Predation by spiders will be addressed in more detail later; however predation by spiders specifically of emerging adults was reported by Onyeka (1983) from artificial containers and permanent freshwater, and by Yates (1979) from tree-holes. *Meta segmentata* [orb-web spider] (Argiopidae) showed evidence of predation on *Culex* spp. emerging from permanent freshwater ponds (7/38) and artificial containers (1/4) (Onyeka, 1983), and *Meta mengai* on an emerging or ovipositing *Ae. geniculatus* that had flown into a web that had been constructed across a tree hole (Yates, 1979). Another tree-hole associated spider (*Anyphaena accentuata*) showed no evidence of predation. Onyeka (1983) also reported predation on *Culex* spp. emerging from ponds by Lycosidae: *Pirata piscatorius* (3/17) and Theridiidae: *Theridion ovatum* (1/10).

Predators of adults resting in vegetation

Apart from the periods of active flight, much of the adult mosquito's time is spent resting in vegetation. During this period of rest, adults are exposed to predation by a number of different species of arachnid from various families. Service (1973a) collected a total of 645 gut smears from arachnids by sweep-netting vegetation from *Oc. cantans* habitats at Monks wood, Ham Street wood and Arne in Dorset. In total, evidence of predation on resting *Oc. cantans* was reported in six out of eight spider families sampled (Argiopidae, Linyphidae, Thomsicidae, Lycosidae, Theridiidae and Tetragnathidae positive; Clubionidae and Pisauridae negative) and from Opiliones [harvestmen].

These included in Argiopidae [orb spiders]: 46/192 *Meta segmentata*, 1/2 *Cyclosa conica* [orb-weaver spider] and 0/5 *Araneus cucurbitinus*; in Linyphidae [money spiders]: 8/41 *Linyphia peltata*, 2/3 *L. triangularis*, 1/1 *L. hortensis,* 3/11 *L. clathrata*, 1/1 *Erigone promiscua* and 0/3 *Hypomma coruntum*; in Thomiscidae [crab spiders]: 1/6 *Xysticus lanio*; in Lycosidae [wolf spiders]: 3/16 *Lycosa amentata* [meadow spider] and 2/4 *Pirata piraticus*; in Theridiidae [comb-footed spiders]: 4/25 *Theridion ovatum*, 5/24 *Theridion sisyphium* [mothercare spider] and 3/9 *Theridion lunatum*; in Tetragnathidae [long-jawed orb weaver spiders]: 13/81 *Tetragnatha montana* and 20/57 *Tetragnatha* spp.; with no evidence of predation in Clubionidae [sac spiders]: 0/4 *Clubionia trivialis* or Pisauridae [nursery web/fishing spiders]: 0/2 *Pisaura mirabilis* and 0/1 *Dolomedes fimbriatus*. In addition, 30/121 unidentified spiders were positive, suggesting that spiders are important predators of mosquitoes resting in vegetation. Service (1973a) also reported that a high proportion of Opiliones gave a positive reaction, but few (36) were tested - these included positive results for 3/13 *Leiobunum rotundum*, 4/9 *Leiobunum blackwalli* and 4/14 unidentified species.

Snow observed several species of spider taking resting adult mosquitoes in Chingford, London (Snow, unpublished), these included: *Amaurobius ferox* (Amourobiidae) [lace weaver spider], *Araneus diadematus* (Araneidae) [garden spider], *Linyphia hortensis* (Linyphiidae), *Meta segmentata* (Tetragnathidae), *Neriene montana* (Linyphiidae), *Ozyptila atomaria* (Thomisidae), *Pardosa pullata* (Lycosidae), *Pisaura mirabilis* (Pisauridae) [nursery web spider], *Salticus scenicus* (Salticidae) [zebra spider], *Tetragnatha montana* (Tetragnathidae). Snow (unpublished) also observed predation by the cobweb spiders *Tegenaria domestica* and *Tegenaria duellica/saeva* (both Agelenidae) in dwellings also in Chingford.

Predators of flying adults

The only reference to predators of flying mosquitoes by invertebrates is of a species of *Tachydromia* (Empididae) on *Anopheles plumbeus* at Brownsea Island in Dorset (Service, 1967). Many other flying insects, such as dragonflies and damselflies are widely known to prey on flying mosquitoes (British Dragonfly Society, 2007). Little quantitative information also exists in the entomological press on the impact of feeding birds and bats on flying adults. Snow (unpublished) observed predation of flying adult mosquitoes in Chingford by *Apus apus* [swift], *Delichon urbica* [housemartin] and *Hirundo rustica* [swallow], and of emerging *Oc. cantans/punctor* in Epping Forest by *Anas platyrhnchos* [mallard]. Additional qualitative information from English Nature (2006), based on observation, suggest that the predominant mosquito feeding bird species are *Delichon urbica*, *Anthus pratensis* [meadow pipit], *Ficedula hypoleuca* [pied flycatcher], *Hirundo rustica*, and *Apus apus*, with other insectivorous species also likely to feed on mosquitoes: *Parus* *caeruleus* [blue tit], *Phylloscopus collybita* [chiffchaff], *Periparus ater* [coal tit], *Regulus regulus* [goldcrest], *Motacilla cinerea* [grey wagtail], *Carduelis cannabina* [linnet], *Aegithalos caudatus* [long-tailed tit], *Anas platyrhynchus* [mallard], *Parus palustris* [marsh tit], *Parus montanus* [willow tit], *Gallinula chloropus* [moorhen], *Motacilla alba* [pied wagtail], *Carduelis flammea* [redpoll], *Carduelis spinus* [siskin], *Muscicapa striata* [spotted flycatcher], *Sylvia communis* [whitethroat], *Phylloscopus trochilus* [willow warbler], *Troglodytes troglodytes* [wren] and *Emberiza citronella* [yellowhammer].

English Nature (2006) also identifies four bat species as mosquito predators: *Myotis nattereri* [Natterer's bat], *Myotis mystacinus* [Whiskered bat], *Myotis daubentonii* [Daubenton's bat] and *Pipistrellus pipistrellus* [Pipistrelle bat]. The latter two species were observed by Snow (unpublished) to feed on flying insects in his studies in Chingford, London. There is little doubt that for some bat species, the abundance of flying mosquitoes at dusk makes them a valuable food source.

Predators of hibernating adults

Female *Cx. pipiens* and *Cx. torrentium* hibernate through winter in cool buildings and various studies have investigated the impact of predators in hibernation shelters. Service (1968) and Sulaiman & Service (1983) observed spiders preying on hibernating *Culex* spp. on Brownsea Island and at West Kirby (Merseyside), and Onyeka & Boreham (1987) also investigated gut smears at Silwood Park.

Several spider species were observed feeding on hibernating mosquitoes in shelters on Brownsea and at West Kirby (Service, 1968; Sulaiman & Service, 1983), including *Meta segmentata, Meta merianae* (both Tetragnathidae), *Tegenaria silvestris, Tegenaria atrica,* (both Agelenidae) *Lepthyphantes leprosus* (Linyphiidae) and *Amaurobius* spp. (Amourobiidae). The guts of spiders collected from the walls of hibernation sites by Onyeka & Boreham (1987) were examined for evidence of predation on *Culex* spp. All three spider species present were predators of mosquitoes: 18/28 *Amaurobius ferox* (Amaurobiidae), 12/39 *Scytodes thoracica* [spitting spider] (Scytodidae) and 13/22 *Tegenaria domestica* [house spider] (Agelenidae). Onyeka & Boreham also sampled five reduviid bugs [assassin bugs] (*Empicoris vagabundus*), but none showed any evidence of predation. Although not strictly predation, on Brownsea Island, Service (1968) collected Collembola [springtails] from the floor of the shelter and found that they had fed on mosquitoes that had died during hibernation. Collembola species found to have mosquito scales in their gut included: *Lepidocyrtus curvicollis, Lepidocyrtus cyaneus* and *Hypogastrura purpurescens*.

Parasites and infections of British mosquitoes

A number of papers have reported on the infections and parasites of the various stages of British mosquitoes. These include viruses, ciliated epibionts, parasitic nematodes, hydrachnids [water mites], microsporidia, vorticellids and various fungi.

The earliest evidence of parasites of British mosquitoes by Marshall & Staley (1929) reported the presence of larval mites (hydrachnids) on *Ochlerotatus annulipes* Meigen and *Aedes cinereus* Meigen collected in Birmingham, which were similar to mites found the previous year attached to *Anopheles maculipennis* and *Oc. cantans* at Hayling Island. They reported the presence of dark, serpentiform, tubular processes, originating at the points where the mouthparts of the larval mite were attached to the mosquito host, and penetrating within the abdomen to distances varying from 0.5-1.0mm. Some of the tubes had no mites, and although most of the tubes had their origin on the dorsal side of the abdomen, some were found ventrally. Marshall & Staley (1929) concluded that these tubes were the product of a protective reaction occurring in the mosquito to oppose some kind of infective invasion originating in the bite of the parasite. Later, Marshall (1938) remarks that owing to their bright red colour, the larval mites are very easily detected, and that these parasites were thought to have taken up their position on the surface of the pupa, ready to transfer themselves to the adult, during emergence. Marshall (1938) reported two species of hydrachnid known to infest British mosquitoes: *Diplodonthus despiciens* on *Ochlerotatus rusticus* (Rossi) and *Oc. cantans*, and *Lebertia tauinsignata* on *An. maculipennis* s.l., *An. claviger, Ae. cinereus, Oc. annulipes* and *Culiseta morsitans* (Theobald). *Diplodonthus despeciens* appeared to attach both to the thorax and abdomen

European Mosquito Bulletin, 25 (2008), 1-11.
Journal of the European Mosquito Control Association
ISSN1460-6127; www.europeanmosquitobulletin.com
First published online 30 April 2008

and *L. tauinsignata* to the abdomen only, with as many as 12 seen on one mosquito.

Later, Service conducted studies on hydrachnids on Brownsea Island (Service, 1968) and in Monks wood (Service, 1973b). On Brownsea (Service, 1968), infestation rates were 24/718 on *Oc. cantans* (range 1-9, mainly attracted to the neck and thorax), 9/750 *Culiseta annulata* Schrank (1-5 mites on the thorax), 3/6000 *Oc. punctor* (1-2 mites on thorax), 1/92 *An. claviger* (one mite on ventral abdomen), and 2/6500 *Oc. detritus* (2 or 3 on thorax). In studies carried out principally on *An. claviger* by Service (1973b) at Monks wood and Surlingham Fen in Norfolk, 4/615 at Monks wood had mites, with a total of 1673 individuals infested at Surlingham. The rate of mite infestations varied seasonally, higher in September (59-61%) than July (6-12%), and was most likely correlated with the seasonal incidence of the mite, with the level of infestation ranging from 1-18, with most females having six. Of the adults examined at Surlingham, 90.4% had mites restricted to abdominal tergites II and III, 8.2% has some mites on the sternites and 1.3% at the base of the thorax. The species of larval mite identified by Marshall (1938) was questioned although not named, by Service (1973b). Furthermore, Ramsdale & Snow (1995) considered these mite infestations benign.

Marshall (1938) also reported on the activities of the ciliate *Glaucoma pyriformis* found in the body cavity of *Cs. annulata* and of unidentified species of the microsporidian genus *Thelania* in larvae of *Oc. punctor* and fat bodies of adult *Oc. punctor, Oc. detritus, Cs. annulata, Culiseta subochrea* (Edwards) and *Cx. pipiens*. The parasitized larvae reportedly died at the end of the 4th instar, the pupa apparently lacking the energy required for rupturing the larval skin. Other protozoal infections epibotic on larvae of *Aedes/Ochlerotatus* spp. were reported by Brown (1949), with vorticellids appearing to infect *Oc. cantans* and *Oc. punctor*. Brown found no adverse effects of the larvae, and resistance to infection appeared to increase in later instars with pupae apparently immune.

Various fungal infections have also been identified and Marshall (1938) reported on two fungal parasites of mosquitoes on Hayling Island: one from each of the families Saprolegniaceae, which was fatal to larvae of *Ae. geniculatus, Oc. rusticus, Cs. annulata* and *Cs. moristans*, and Entomophthoraceae, probably *Empusa culicis* - fatal to adults of *Oc. detritus* and *Cx. pipiens*. Service (1968) reported on at least two fungi, *Cephalosporium* sp. (possibly *C. coccorum*) and *Entomophthera* sp. nr *conglomerate*, which caused considerable mortality to hibernating *Cx. pipiens* on Brownsea. Dead mosquitoes found in the same shelters were also infected with saprophytic *Penicillium, Mucor* and *Sporotrichum* sp. Fungal infections of *Oc. cantans* larvae caused by *Coelomymces* nr. *psorophorae* were also reported by Service (1977) in Monks wood, with an infection rate of <1%, with those infected usually succumbing prior to pupation. In the same study, Service (1977) found *Oc. cantans* larvae infected with up to three parasitic nematodes, attacking and killing both the larvae, and the adult shortly after emergence. Ramsdale & Snow (1985) reported that parasitic nematodes of Mermithidae [eel worms] invariably kill the host.

Viral infections have been reported in British mosquito larvae. Two larvae showing a lime-green colour were collected from a small pond at Ham Street wood by Tinsley *et al*. (1971) which were found to be infected with a virus of the iridescent group. Eleven similarly infected late 3rd and 4th instars were later found, developing the same lime-green colour at an advanced stage of infection. Service & Streett (1976) were able to quantify the level of infection in *Oc. cantans* larvae collected at several sites in Monks wood, where yearly a small percentage (0.1-2.3%) of 4th instar larvae collected in spring and summer were infected. An additional virus was attributed to larval deaths of mosquitoes by Goldie-Smith (1987) whilst working on Dixidae, with mosquito larvae succumbing when introduced into dishes of larvae of certain Dixidae infected with cytoplasmic polyhedrosis virus (CPV).

Plants that naturally inhibit mosquitoes

Ramsdale & Snow (1995) reported records in Europe of certain mosquito species being devoured by carnivorous plants, however, it is unclear whether native sundews and butterworts reduce mosquito numbers. *Azollaceae* [water fern] and *Lemna* spp. [duck weed] however, can quickly completely cover the water surface, tending to preclude mosquito larvae, and these may be useful in artificial container water butts in gardens. Two species of *Azolla* (*A. filiculoides* and *A. caroliniana*) have been introduced from North America and are established in Britain.

Conclusion

Although the impact of insect and arachnid predators may be marginal, it is important that these predators are maintained within mosquito habitats. Care must be taken not to reduce their numbers by environmental manipulation or agricultural pesticide use. Ways should be considered to enhance their numbers by making habitats more suitable for their survival. It is important that any measures to control mosquitoes take into account the need to maintain natural predators and their habitats. Removal of predators from habitats could exacerbate a mosquito nuisance biting problem. We conclude that the most effective predators would appear to be fish. These may be introduced and maintained in suitable habitats, including natural waters and ornamental ponds.

References

Beattie, M.V.F. & Howland, L.J. (1929) The bionomics of some tree-hole mosquitoes. *Bulletin of Entomological Research,* **20**, 45-58.

British Dragonfly Society (2007) http://www.dragonflysoc.org.uk/frameset.htm?home&home Accessed 17 July 2007.

Brown, E.S. (1949) Vorticellids epibiotic on larvae of the genus *Aedes*. *Entomologist's Monthly Magazine,* **85**, 31-34.

English Nature (2006) www.plantpress.com/wildlife/home.php Accessed 29 December 2006.

Goldie-Smith, E.K. (1987) Virus infections of larval Dixidae and other Culicoidea (Diptera: Nematocera). *Entomologist's Gazette,* **38**, 137-139.

Jeffries, M. (1988) Individual vulnerability to predation: the effect of alternative prey types. *Freshwater Biology,* **19**, 49-56.

Jenkins, D.W. (1964) Pathogens, parasites and predators of medically important arthropods. *Bulletin of the World Health Organization,* **30**, 150pp.

Kitching, R.L. (1971) An ecological study of water-filled tree-holes and their position in the woodland ecosystem. *Journal of Animal Ecolog,y* **40**, 281-302.

Lockwood, A.P.M. (1986) *Gammarus duebeni* as a predator of mosquito larvae. *Porcupine Newsletter,* **3**, 201-203.

Marshall, J.F. (1938) *The British mosquitoes*. British Museum (Natural History) London. 341pp.

Marshall, J.F. & Staley, J. (1929) A newly observed reaction of certain species of mosquitoes to the bites of larval hydrachnids. *Parasitology,* **21**, 158-160.

Molenkamp, A.N. (1998) Seasonal emergence pattern, sex ratio and biological control of the saltmarsh mosquito, *Aedes detritus* (Haliday). University of East London. M.Phil. Thesis

Onyeka, J.O.A. (1983) Studies on the natural predators of *Culex pipiens* L. and *C. torrentium* Martini (Diptera: Culicidae) in England. *Bulletin of Entomological Research* **73**: 185-194

Onyeka, J.O.A. & Boreham, P.F.L. (1987) Population studies, physiological state and mortality factors of overwintering adult populations of females of *Culex pipiens* L. (Diptera: Culicidae). *Bulletin of Entomological Research* **77**: 99-112

Ramsdale, C.D. & Snow, K.R. (1995) *Mosquito Control in Britain* University of East London. 100pp

Roberts, G.M. (1995) Salt-marsh crustaceans, *Gammarus duebeni* and *Palaemonetes varians* as predators of mosquito larvae and their reaction to *Bacillus thuringiensis subsp. israelensis*. *Biocontrol Science and Technology* **5**: 379-385

Service, M.W. (1967) *Tachydromia* spp. (Diptera: Empididae) as predators of adult anopheline mosquitoes. *Entomologist's Monthly Magazine* **104**: 250-251

Service, M.W. (1968) Observations on the ecology of some British mosquitoes. *Bulletin of Entomological Research* **59**: 161-194

Service, M.W. (1973a) Study of the natural predators of *Aedes cantans* (Meigen) using the precipitin test. *Journal of Medical Entomology* **10**: 503-510

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

Service, M.W. (1977) Ecological and biological studies on *Aedes cantans* (Meig.) (Diptera: Culicidae) in southern England. *Journal of Applied Ecology* **14**: 159-196

Service, M.W. & Streett, D.A.. (1976) A pathogenic mosquito iridescent virus in *Aedes cantans*. *Transactions of the Royal Society for Tropical Medicine & Hygiene* **70**: 18

Sulaiman, S. & Service, M.W. (1983) Studies on hibernating populations of the mosquito *Culex pipiens* L. in southern and northern England. *Journal of Natural History* **17**: 849-857

Tinsley, T.W., Robertson, J.S., Rivers, C.F. & Service, M.W. (1971) An iridescent virus of *Aedes cantans* in Great Britain. *Journal of Invertebrate Pathology* **18**: 427-428

Yates, M.G. (1979) The biology of the tree-hole breeding mosquito *Aedes geniculatus* in southern England. *Bulletin of Entomological Research* **69**: 611-628