Review

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Could species-focused suppression of *Aedes aegypti*, the yellow fever mosquito, and *Aedes albopictus*, the tiger mosquito, affect interacting predators? An evidence synthesis from the literature

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Abstract

The risks of *Aedes aegypti* and *Aedes albopictus* nuisance and vector-borne diseases are rising and the adverse effects of broad-spectrum insecticide application have promoted species-specific techniques, such as sterile insect technique (SIT) and other genetic strategies, as contenders in their control operations. When specific vector suppression is proposed, potential effects on predators and wider ecosystem are some of the first stakeholder questions. These are not the only *Aedes* vectors of human diseases, but are those for which SIT and genetic strategies are of most interest. They vary ecologically and in habitat origin, but both have behaviorally human-adapted forms with expanding ranges. The aquatic life stages are where predation is strongest due to greater resource predictability and limited escape opportunity. These vectors' anthropic forms usually use ephemeral water bodies and man-made containers as larval habitats; predators that occur in these are mobile, opportunistic and generalist. No literature indicates that any predator depends on larvae of either species. As adults, foraging theory predicts these mosquitoes are of low profitability to predators. Energy expended hunting and consuming will mostly outweigh their energetic benefit. Moreover, as adult biomass is mobile and largely disaggregated, any predator is likely to be a generalist and opportunist. This work, which summarizes much of the literature currently available on the predators of *Ae. aegypti* and *Ae. albopictus*, indicates it is highly unlikely that any predator species depends on them. Species-specific vector control to reduce nuisance and disease is thus likely to be of negligible or limited impact on nontarget predators.

Keywords: ecology; environmental impact assessment; Zika; dengue; vector control; SIT; IIT; genetic insect control

1 INTRODUCTION

Almost 200 years since the first formal links were made between the transmission of yellow fever and mosquitoes (Beauperthuy 1854 cited in reference 1), we are still working to understand and manage these vector species. The risks of both *Aedes* spp. nuisance and of their vector-borne diseases are rising with both urbanization and the climate-driven range alteration of these mosquito species, and over a billion people are now considered to become vulnerable to their first exposure to *Aedes*-borne viral diseases over the coming century.[2] The economic consequences of this nuisance and disease are substantial, with estimates of global total costs in yellow fever virus and dengue virus as high as 57.3 billion USD,[3] and those predicted for a single epidemic of Zika virus (through medical costs and productivity loss) rising to almost a billion USD in the southeast USA alone.[4] The genus *Aedes* is the most costly invasive animal taxon, with damage and management costs estimated at 150 billion USD between 1970 and 2017.[5] These estimates do not always reflect the full human and public health costs, nevertheless they underpin the need for investment in vector control.

An increased understanding of the adverse effects of broad-spectrum insecticide applications on ecosystem and human health has driven the exploration of species-focused controls which are more precise in their mode of action. Following the use of narrow-spectrum biopesticides such as *Bacillus*

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thuringiensis var israelensis (Bti), which have reduced ecological impacts, the more precise sterile insect technique (SIT), the insect incompatibility technique (IIT) and molecular genetic control methods are now becoming contenders in *Aedes* spp. vector control operations.[6–8] Carefully considered and well-planned species-specific control programs are essential to ensure reductions of the target vector populations and influence health-related outcomes.[9] Most are, however, spatially and temporally limited designs which do not include assessment of the potential for dynamic feedbacks across trophic levels.

Mosquitoes have a number of predators that collectively may exert some influence on reducing mosquito numbers, although, with a very few exceptions, predators generally have little effect on mosquito abundance over a large area. Despite this observation, one of the first questions asked by stakeholders of any species management program such as SIT, or more recent molecular transgenic techniques, concerns the effect on the local ecology of either the releases themselves or of a reduction (elimination) of the mosquito species addressed.[9] There are two principal ecological situations in which these questions arise: the first is within the species' original ranges where interspecific community relationships are established, the other is in recently invaded locations where the interspecific interactions are novel and may themselves be disruptive to the existing native ecosystem.[10] Using specific vector control methods to prevent or push back an expanding invasive wave front is thus of lesser ecological concern than applications within their established ranges. Nonetheless, a synthesis of the current understanding of the ecological relationships of these mosquitoes is overdue and may be useful to both situations.[9] The two species addressed here are not the only vectors of viral disease in the *Aedes* genus, but are those for which SIT and genetic controls are of most interest.[6]

We hope here to provide a foundation on which to base answers to some of the ecological questions posed of specific control activities and to identify areas for future research into the community relationships of these mosquitoes. This work summarizes much of the academic literature currently available on the community interactions of *Aedes aegypti* and *Aedes albopictus* focusing specifically on their identified predators (largely from biological control studies). The larval habitat is the principal limiting resource phase for these mosquitoes and one in which competition, both intra- and interspecific, will act most intensively. The aquatic life stages are also where the influence of predation may be strongest due to resource predictability and limited escape opportunity. As adults the *Aedes* spp. are average-sized mosquitoes, although foraging theory predicts similarly to the smaller anophelines that they are of low profitability to predators.[11,12] The energy expended hunting, handling and consuming would, unless they were predictably and densely aggregated, outweigh the energetic benefit of consuming them. The adult biomass is mobile and largely disaggregated, and while many predators may consume these mosquitoes it is generally considered that these are generalist, opportunist predators.[12] Much of the actual, and predicted future, range expansion is into more temperate, seasonally variable zones and the mosquito biomass available to predators will be increasingly seasonal in pattern.[13] This seasonality is largely driven by the interaction of temperature regime and water availability and, along with permanent water bodies, opportunistically available human-associated containers and pools which rarely host aquatic predators become ideal larval habitats for *Aedes* spp.[14] The broad consensus, which we examine here, is that most mosquito predators are generalists[15–17] as any specialism would be a high-risk strategy given the constraints above.

1.1 Brief overview of the biology and ecology of the target species

Ae. aegypti, once considered native to African forests but which is now thought to originate in the southwest Indian Ocean region, has two broad forms; a sylvan form for which the dominant larval habitat is tree holes and other naturally occurring containers, and the ecotonal, feral form, which has adapted to our multitude of incidental, artificial or man-made containers.[18–21] This latter is the form of most concern as it is anthropophilic, has a day and crepuscular biting habit, and has a tendency to rest inside houses, which link its range expansion to human populations.

Ae. albopictus, a native animal of Asian forests, varies widely in preference for human blood across its broad distribution, but shows increased anthropophily near human populations.[22] This mosquito can inhabit a wide variety of habitats, is resilient to a wide range of conditions and, in temperate regions, their eggs can diapause until suitable environmental conditions for larval development arrive. In 1988 Hawley noted that *Ae. albopictus*, an ecological generalist, is characterized by its variability and capacity, with human help, to rapidly colonize new habitats, this view is being borne out by the continued pattern of range expansion.[23]

In the Aedini tribe, which includes these species, typically 50–120 eggs are laid at the edge of water or in flood-prone moist areas. The eggs of both species can survive many months, and even years, of desiccation and it is this which is thought to have been key to their rapid range increase via incidental human transport of desiccated eggs.[24] When moisture and temperatures are favorable, their larvae can develop rapidly in very small water volumes.[23,25] Artificial containers such as plant pots, bowls and discarded containers found near human habitations are ideal nurseries. Larvae have four instars followed by a mobile pupal phase and all can display predator avoidance behaviors. The speed of development is temperature-dependent, but can be as rapid as 5 days between egg hatch and adult.[1] The composition and density of larval mosquito communities are strongly influenced by the ephemeral or permanent nature of the larval habitat and the exposure to predation and competition in these phases is environmentally extremely variable.[19,26]

Anthropic adult female *Ae. aegypti* live in dark and shaded places near and in houses where they have increased opportunity to blood feed on human, and sometimes other vertebrate, hosts. *Ae. albopictus* are mostly outdoor-living and will feed more readily on other vertebrates, which permits them to live further from humans in natural habitats such as neighboring woodlands and damp areas.[25] In both species the adult males feed on plant nectars and similar, but remain close to females through habitat preference and an attraction to blood meal hosts, which together serve to increase their mating opportunity. The individual flight dispersal distances of these species depend on the ecological context and hospitality of the environment. Adult dispersal has been estimated in a number of situations and, although substantially longer distances are recorded, a general consensus suggests that they rarely move more than 100 m from their larval habitat, especially when living near humans.[18,27,28] The body size of an adult mosquito depends on developmental circumstances such as larval density and food availability[29]; although there is much variation, *Ae. aegypti* have a typical body length of 3–4 mm and *Ae albopictus* one of 4–6 mm.[24,25,30]

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1.2 A comment on competition

There exists a substantial literature on competition between these, and other, mosquito species as well as with other, largely herbivorous, animals which share the larval habitats. This comes from two general source categories; reductive and specific studies in controlled environments such as replicated containers in laboratories (e.g. references 31–33) and field ecology counts, which may draw their inference from actual vector control operations or pre-post invasion data.[34–36] Laboratory studies are tractable, but have less potential for generalization; field studies may be more realistic, but present many measurement challenges with substantial temporal and spatial pattern variation leading to some caution in interpreting their data at wide scales.[37] The interplay of predation and competition experienced in the larval habitat is complex and each factor may differentially and contextually affect the developing larval instars.

Evidence is growing of interspecific reproductive interference (satyrisation) acting as part of competitive displacement by *Ae. albopictus* of *Ae. aegypti* in the peri-human habitats where they overlap.[38,39] This effect may well influence the risks of the diseases borne by these vector species and suggests that it is not only at the larval stages that competition is influential. A full review of the existing *Aedes* spp. competition literature would help to promote a greater understanding of the potential ecological consequences of range contractions caused by vector control interventions or of range expansions by *Ae. aegypti* and *Ae. albopictus*, but this is beyond the scope of this review.

2 METHODS

We review the literature available on the ecological interactions of *Ae. aegypti* and *Ae. albopictus* focusing on their predators in natural habitats in order to summarize current knowledge. All papers cited were reviewed, but not all of the works that may have preceded or surrounded these investigations have been included. We do not claim to have been exhaustive and the presentation of all studies is beyond the capacity of this review. Where relevant, such as with birds and bats, the predation of mosquitoes more widely is included. The aim of this paper is to provide an overview of the predator organisms already considered in the literature, and to support discussions on the potential ecological implications of any vector control initiative that seeks specifically and precisely to reduce populations of these mosquitoes.

Peer-reviewed scientific literature, relevant internal reports and web-based resources were searched to identify *Aedes* spp. predators. Topic search terms, used individually and in combination, included 'Aedes', Predator, Natural Predator, Natural Prey + *predator species*, precipitin. Review and predator ecology articles were included, and further relevant papers found therein were additionally traced to extend the reach. The Web of Science, Google Scholar, Google and Mendeley databases were all used to explore the field. Searches took place during April–August 2021. The authors also consulted senior subject specialists (see Acknowledgements section) and through this route accessed some much earlier foundation literature. The mosquito ecology literature is diverse and reflects the spectrum of study approaches that range from controlled microcosm laboratory experiments to extended field investigations. Putative predators in field contexts have been explored using a range of techniques from simple observations through radio-tagged prey, precipitin immunological assays to molecular barcoding.[40–42] Microcosm laboratory studies can provide an indicative baseline from which to characterize ecological interactions. Extrapolations or inferences on the strength and stability of an ecological linkage from these should, however, be weighted cautiously. Feeding preferences evaluated in such simple settings cannot provide evidence of a dependence or even a requirement as part of a natural diet. The competitive environment and what a predator eats in the field are variable and reflect environmental conditions, as well as inherent decision making by individual animals.

3 RESULTS

3.1 Egg predation

The eggs of these species can be desiccated, partially desiccated or moist and found either in water or above a water line on dry land. This creates substantial opportunity for predation in natural environments and smaller predators, such as other invertebrate species, may receive an energetically valuable dietary component from mosquito eggs. In anthropic forms, the potentially short duration of the egg phase in water-filled transient container sites limits the predation risk in this phase for mosquitoes living near human habitations.

3.1.1 By invertebrates

Predatory *Toxorhynchites* spp. mosquitoes, including *Toxorhynchites splendens*, which has been deployed as a biocontrol agent for *Aedes* spp. mosquitoes principally at the larval life stages (see the larval predation section below), will consume both its own and other species' eggs when starved for 24 h *a priori* in laboratory conditions. Their cannibalism rates fell when the eggs of other species (*Ae. aegypti* and *Anopheles stephensi*) were supplied.[43] Analysis of the natural prey of *Toxorhynchites rutilus*, identified and quantified from gut contents via microscopy of exoskeletal remains, found a number of dipteran eggs. This provided data on the frequency of occurrence that indicated little energetic importance to such a predator. A dipterous larva is, for example, of greater nutritional value than an egg for the growth and development of a *Toxorhynchites* larva. This suggests that although these species may predate on mosquito eggs, and cannibalize their own, it is unlikely a large part of their diet and even less likely that any egg predator is monophagic or even stenophagic.[44]

Psocids (Booklice: Psocoptera; Liposcelididae) are globally distributed, common scavengers thriving in warm, damp environments, making insectaries ideal habitats. The discovery of egg predation by *Liposcelis bostrychophila* was triggered by issues in an *Aedes* insectary. This Psocid feeds on the egg chorion and not the embryo inside, although the damage leads to embryo mortality due to dehydration.[45]

An investigation into predation by *Solenopsis invicta* (the red imported fire ant: Hymenoptera; Formicidae) found they punctured and fed on *Ae. albopictus* eggs in the laboratory. The presence and actions of the ants, especially the minima workers, reduced the hatching of egg populations.[46] A field investigation of the predation of dormant *Ae. aegypti* eggs in a temperate region of Argentina found that ants of the genus *Strumigenys* (Hymenoptera; Formicidae), the isopod *Armadillidium vulgare* (pill-bug: Isopoda; Armadillidiidae) and the dermapteran *Euborellia annulipes* (ring-legged earwig: Dermaptera; Anisolabididae) were associated with a high proportion of lost eggs. In laboratory conditions, *A. vulgare* and *E. annulipes* consumed the offered eggs and confirmed their predatory capacity. This study is the first record of predation of *Ae. aegypti* eggs in temperate South America and the first evidence of earwigs consuming mosquito eggs.[47]

The beetle *Curinus coeruleus* (blue lady beetle: Coleoptera; Coccinelidae), a biological control agent of the coconut mealybug *Nipaecoccus nipae* (Hemiptera; Pseudococcidae) and the psyllid *Heteropsylla cubana* (Hemiptera; Psyllidae), was examined for its ability to consume *Ae. albopictus* eggs in the laboratory. Over 70% of *C. coeruleus* larvae in this test preyed on *A. albopictus* eggs, consuming over 50 eggs per instar. The beetle larvae survived for 5–6 days, but could not complete its life cycle by feeding only on *Ae. albopictus* eggs. These eggs, which are available year-round in Hawaii, may be a supplemental food source for *C. coeruleus* larvae when there is a shortage of psyllids.[48] In another natural setting, observed predation by *Periplaneta americana* (the American cockroach: Blattodea; Blattidae) was a major cause of *Ae. aegypti* egg loss in surface sites in Australia.[49]

3.1.2 By vertebrates

The eggs of mosquitoes are minute,[50] and *Ae. aegypti* and *Ae. albopictus* lay individual eggs as opposed to the egg rafts made by some *Culex* species, thus egg predation by predators may be lesser, or simply less apparent.[51] Some vertebrate predation of *Aedes* and other mosquito species eggs has also been recorded in laboratory experiments. Although predation by *Ommatotriton vittatus* (the southern banded newt: Urodela; Salamandridae) was rare, even in mesocosms,[52] video observations substantiate that tadpoles can be active predators of *Aedes* spp. eggs.[53] This work showed that the tadpoles of five species from randomly selected, representative amphibian (frog and toad) genera (*Bufo*, *Euphlyctis*, *Hoplobatrachus*, *Polypedates* and *Ramanella*) can be mosquito egg predators. Direct observations[53] confirm that many tadpole species are mosquito egg predators. With about 7000 frog species worldwide, living in a diversity of aquatic habitats including many that fish cannot reach, the role of tadpoles in mosquito ecology may be greater than currently understood, but mosquito eggs are unlikely to be a substantial food source for these predators. Fish are also likely to be opportunistic consumers of *Aedes* spp. eggs, although these too are likely to be a minor and nonessential dietary component. In mesocosm experiments, free-roaming fish will predate *Culex* spp. mosquito egg rafts.[54]

3.2 Larval predation

In natural and long-lasting aquatic environments, mosquito larvae have a number of predators, including other invertebrates, tadpoles and fish.[15] Known predators have been actively deployed as mosquito biocontrol agents in several settings, with the most widely used being the western mosquito fish, *Gambusia affinis* and the eastern mosquito fish, *G. holbrooki*.[55] The effect of these fish on native faunal composition and their inability to colonize small containers, such as tree holes etc., which are ideal larval habitats of some important vector mosquitoes, make them impractical for controlling populations of the mosquitoes considered here.[56]

Mosquito larval predators do occur in predictable, but temporary, water bodies as well as in permanent ones. A detailed investigation of predation of first- and second-instar larvae of two other *Aedes* species, *Ae. stimulans* and *Ae. trichurus*, in temporary woodland pools used larvae tagged with radioactive phosphorus. From >400 aquatic insects and other animals collected, 28% were identified as preying on the tagged mosquitoes. Among these, eight species of Dytiscidae (diving beetles: Coleoptera), one of Hydrophilidae (water scavenger beetles: Coleoptera), one of Limnephilidae (caddisflies: Trichoptera) and one pond snail (Mollusca; Gastropoda) are regarded as important predators. Three additional species of water beetle were identified as predators from aedine remains in their digestive tracts.[42]

Service's studies of *Ae. cantans* predation at four locations in southern England used a precipitin test on the gut contents of 2893 recently fed possible mosquito predators. Several larval predators were identified, the most important being immature Dytiscidae (diving beetles: Coleoptera), but predation caused little reduction in the size of the larval mosquito population.[57] Survivorship curves calculated for *Ae. cantans* indicated the greatest mortality in the youngest instars and an overall mortality of 95% in overwintering immature stages.[58] Some of this loss was attributed to predation, although a *Coelomomyces* fungi, an indehiscent virus, mermithid nematodes and other infections caused other larval deaths.[58]

In the human-associated, peri-urban container habitats favored by *Ae. aegypti* and frequently also used by *Ae. albopictus*, there is often a reduced animal community as colonizing these is challenging and their ephemerality (frequent drying-out) discourages establishment. This reduces the likelihood of predation and competition may be a stronger structuring effect in this habitat type.[12,59]

3.2.1 By plants

Not all predators are animals. Plants such as the fly traps and pitcher plants are carnivorous and also consume insects. The common bladderwort *Utricularia macrorhiza* (Lentibulariaceae) and other related species use ‘bladders’ to capture small aquatic organisms. Hairs at the bladder-mouth serve as triggers, mechanically causing the trap to spring open, sucking in water and adjacent organisms. These predatory plants have been evaluated as potential larvicidal agents of *Ae. aegypti* and *Ae. albopictus* in no-choice, laboratory experiments. The predation efficiency and facultative predation strategy they display may warrant further study in the field of larval mosquito control.[60] There is, however, no evidence of their dependence on mosquito larvae, and they consume many phytoplankton and gain other nutrients from the soil.

3.2.2 By invertebrates

3.2.2.1. Arachnida – Aranae and Acari: spiders and mites. Aranae: The spiders feeding in and around aquatic habitats are diverse; most that prey on mosquito larvae are active hunters that do not build webs. These spiders can be terrestrial, standing at the water's edge, semi aquatic, surface film locomotors or subsurface divers which use air sacks.[12] One spider, a southeast Asian jumping spider, *Paracyrba wanlessi* (Salticidae), lives principally in fallen bamboo preys on the larvae, pupae and adults of mosquitoes. This spider chooses mosquitoes more often than a variety of other prey types, regardless of whether the prey are in or away from water, and regardless of whether the mosquitoes are adults or juveniles. This preference for mosquito larvae, pupae and adults remained despite exposure to experimental variation in diet.[61]

The fishing spider *Dolomedes triton* (Pisauridae) is an active predator of mosquito larvae at the water's surface, although there is no specific evidence of *Aedes* spp. consumption.[62] Similar is true of many spiders identified as predators of aquatic dipteran larvae and a number of studies, for example that of Perevozkin and colleagues, who[63] used *Anopheles* spp. and *Culex* spp. mosquitoes to study the foraging behavior of spiders of the genera *Argyroneta*, *Dolomedes*, *Pirata* and *Pardosa confirm this*. In most cases, there is no reason to think these species, and other Aranae, would not also take *Aedes* spp. larvae, but this has rarely been demonstrated outside of laboratory assays.

Acari: This extraordinarily diverse taxon of mites and ticks has fully aquatic members in which the nymphs and adults can be free living. At a site in India, *Arrenuris madaraszi* mites were found feeding on approximately 20% of *Anopheles* spp. mosquitoes and could fully complete their life cycle in the laboratory using *Ae. albopictus* as hosts. The host specificity of these parasitic mites is thus likely ecological, not physiological and in the laboratory, nymphs and adult mites showed some preference for first-instar mosquito larvae, particularly those of *Ae. albopictus*.[64]

3.2.2.2. *Coleoptera: beetles*. Often proposed as mosquito biocontrol agents and central to many freshwater aquatic food webs, adult and larval diving beetles (Dytiscidae) are generalist predators, feeding on zooplankton, aquatic invertebrates, larval amphibians and fish. Some dytiscid species display selective predation, cannibalism and intra-guild predation, and have behavioral effects on prey that can shape the food web structure and species composition of established water bodies.[65] Laboratory studies of the predatory impact of the dytiscid beetle, *Rhantus sikkimensis*, on fourth-instar *Culex quinquefasciatus* indicated they consumed between 18 and 35 larvae day^{-1} depending on prey densities, approximately three times the consumption of *Tx. splendens*.[66] Dytiscids of the genus *Platynectes* were observed to invade the rubber plantations of Kerala, India during the monsoon season and voraciously devour the larvae of *Ae. albopictus*. Field investigations showed a reduction of 70.91% ($P = 0.0017$) and 100% in *Aedes* larval density on the first and fourth days post-release of eight beetles per latex collection container, respectively.[67] A polymerase chain reaction (PCR) assay developed to detect the DNA of *Ae. sticticus* and *Ae. vexans* in the guts of medium-sized dytiscid diving beetles identified one or both mosquito species in 14% of field-caught beetles. This underpins that, while these mosquito species are consumed by the dytiscids, these are polyphagous predators.[68]

3.2.2.3. *Crustacea: copepods, cyclops and shrimp*. Freshwater crustaceans, tadpole shrimp and copepods are adapted to temporary bodies of water, particularly in arid zones. Many copepod species employ a seasonal diapause or dormancy strategy and can rapidly recolonize floodwaters and isolated puddles.[69]

Copepoda: As with other taxa, evidence is available from investigations of potential biocontrol agents among the abundant and adaptable carnivorous or omnivorous members of this group. Some cyclopoids have long been known to flexibly use mosquito larvae as food and have an advantage over other aquatic predators as they are 'wasteful killers' and can kill 30–40 mosquito larvae per day more than they actually consume as, if larvae are numerous, they only eat a portion of each.[70]

Field experiments in French Polynesia showed that *Mesocyclops* spp. (Cyclopidae) could reduce larval numbers of *Ae. aegypti*.[71] Subsequently these copepod predators were a key part of a community-based and successful dengue vector control program in Northern Vietnam which effectively eliminated the mosquito vectors from over 11 000 households to become the first example of control of a vector-borne disease by biocontrol.[72,73]

In Nagasaki, Japan, *Macrocyclops distinctus*, *Megacyclops viridis* and *Mesocyclops pehpeiensis* (Cyclopidae) were investigated as biological control agents against *Ae. albopictus*. *Macrocyclops* and the mixture of all three provided better control than either *Megacyclops* or *Mesocyclops* alone. When control containers were at peak larval densities, the overall reduction in those with combined copepods was almost total.[74] In Brazil, water bodies were screened for copepods by collecting 1.5 L of water from each. The predatory potential of the copepods on first-instar *Ae. albopictus* larvae was evaluated over 24 h in the laboratory and ranged from 0% to 97%. A sample collected in the field containing only *Mesocyclops longisetus* var. *longisetus* showed greatest control efficiency, although, in contrast, a sample with few *M. albidus* var. *albidus* was second to this with only 26% efficiency.[75] *Macrocyclops albidus*, released into tires near New Orleans to reduce *Aedes* spp. emergence, was shown to be a promising candidate for control of mosquito larvae because it is a widespread and highly effective predator that is capable of establishing and maintaining populations under a wide variety of field conditions.[76] Fifteen Caribbean strains of copepods were assessed for their predation activity against mosquito larvae. *Macrocyclops albidus*, *Mesocyclops aspericornis* and, as has been seen elsewhere, *M. longisetus* were the most effective against *Ae aegypti* but not against *Cx. quinquefasciatus*.[77] In Australia a decade previously *M. aspericornis* was selected for small-scale field trials as it had proved in trials to be the most effective Queensland predator and exhibited an elevated reproductive rate at 20°–25°.[78] Another trial to estimate field effectiveness of *M. aspericornis* in *Ae. aegypti*-infested wells and mine shafts led to eradication at all five treated sites.[79] Point source inoculation with *Mesocyclops* spp. provided good and persistent control, despite dry periods, of the invasive mosquitoes *Ochlerotatus tremulus* and *Ae. aegypti* in subterranean urban habitats in north Queensland.[80]

Of the 18 species of cyclops collected from aquatic habitats in New Orleans, one third preyed on first-instar *Ae. albopictus* larvae: *Acanthocyclops vernalis*, *Diacyclops navus*, *Macrocyclops albidus*, *Mesocyclops edax*, *Mesocyclops longisetus*.[81] *Mesocyclops longisetus* was again identified as most effective, as it was the most voracious predator and survived best in the containers, later reducing *Ae. aegypti* larvae by >98% compared with control containers.[82] Other laboratory studies of copepods have demonstrated that not all species are effective consumers of mosquitoes. The predatory behavior of *Acanthocyclops vernalis* and *Diacyclops bicuspidatus thomasi* on the first instars of *Ae. canadensis* and *Ae. stimulans* revealed that although *A. vernalis* fed on early instars, it was substantially less effective in the presence of alternate food. Even with no-choice, *D. b. thomasi* did not consume the *Aedes* spp. larvae.[83] There is substantial further variation in preference identified across the Mesocyclops genus: when alternative prey were introduced the >50% consumption over 72 h of *Ae. aegypti* by *M. annulatus*, fell to 16%.[84] This suggests that studies in which between species preferences are revealed in simplified systems, such as the preference for *Ae. aegypti* over *An. stephensi* and *Cx. quinquefasciatus* of *Mesocyclops thermocyclopoides*, should not be extrapolated too conclusively.[85]

The life-history traits and flexible feeding strategy of cyclopids promote their long-term survival in natural habitats.[86] They have a wide spectrum of potential food items available, including dipteran larvae, algae, ciliates, rotifers, cladocerans and copepod nauplii, and many can diapause to persist through inclement seasons. The ability of cyclopids to eat different kinds of foods (omnivory) and the tendency to include a variety of foods in the daily ration may enhance the probability of obtaining a nutritionally complete ration in variable, nutritionally dilute, food environments.[87]

Among non-copepod crustaceans, notostracan tadpole shrimp (Triopsidae) and malacostracan shrimp and prawn are also predators of mosquito larvae. They are important animal groups on many floodplains which may also host mosquito species such as *Ae. albopictus* and *Culex pipiens* and the floodwater specialist *Psorophora columbiae*.[88] The Triopsidae are potential predators adapted to ephemeral aquatic habitats in arid regions and rice paddy fields. Laboratory studies show that very young *Macrobrachium tenellum* (Palaemonidae) prawns will consume 95–100% of *Ae. aegypti* larvae in high density treatments; there is no evidence to link these as predators of *Aedes* spp in the field.[89]

3.2.2.4. Diptera: flies. Some mosquitoes predate on other mosquito larvae; *Toxorhynchites* spp. adults are often called elephant mosquitoes and are larger than *Aedes* mosquitoes. The predatory habits of the larvae may free the adult females from a blood meal requirement and *Toxorhynchites splendens* is one such species. Its larvae feed on the larvae of other mosquito species, while the adults feed on honeydew, fruit and nectar.[90] Natural prey of the predatory mosquito *Toxorhynchites rutilus* were identified from gut contents of 941 larvae collected from tree holes and tires located in an oak-palm woodland in south Florida. Twenty taxa of aquatic prey were recognized in midgut remains. Amid this diversity, mosquito larvae accounted for only 6% of prey items from tree holes and 5% from tires. The remains of terrestrial arthropods of nine insect orders plus mites and spiders were also identified, these prey having been captured from the water surface by voracious *T. rutilus* larvae.[44] *T. splendens* are wasteful predators as, prior to pupation, they kill surplus prey. Laboratory studies showed that when larvae of *Ae. aegypti*, *Anopheles stephensi* or *Cx. quinquefasciatus* were offered to the predator, the number of prey killed, but not eaten, ranged from 0% to 38%.[91] A careful assessment of the value of *Toxorhynchites* spp. in biocontrol of other mosquito species concludes that they have potential in certain restricted but important situations such as urban forest edges in semitropical zones such as in successful trials near New Orleans, LA.[92]

3.2.2.5. Hemiptera: true bugs. Several families of aquatic hemipterans are known to consume mosquito larvae and are described here, although very few of these are found in the container habitats typical of the mosquito species considered here. The water boatmen (Corixidae) are mostly scraper-feeders and, unlike other Hemiptera, have mouthparts capable of ingesting solid food which provides a wide variety of food options and a range of feeding techniques. Many rest attached to the bottom and consume algae and small benthic animals in the detritus. Some genera, *Cymatia* and *Callicorixia* have distinct predatory tendencies and ambush passing prey or pursue prey below the water surface.[93] *Callicorixia audeni* and *C. alaskensis* have been recorded to eat larvae of *Ae. communis* in jars, although these are unlikely to be an important part of their diet in the wild (Sailor & Lienk 1954, cited in reference[93]).

The long-lived (1 year) giant water bug *Belostoma anurum* (Belostomatidae) also readily consumes *Ae. aegypti* larvae, although this takes double the development time (c. 85 days egg-adult) when raised on an arthropod diet *vs* one that includes fish larvae.[94] Intriguingly, in an experimental container *B. anurum* took longer to capture larvae of pyrethroid-resistant *Ae. Aegypti*, which swam for more time and further in predator evasion. This suggests that insecticide resistance may also confer physiological and behavioral changes which reduce predation.[95]

The dominant Heteropteran mosquito predators were identified from water near houses in southern Vietnam. Of 3646 individuals collected, they were most abundant. PCR analysis of their gut contents revealed consumption of *Ae. aegypti* in 40% of *Micronecta* spp. (Corixidae) and 12% of *Microvelia* spp. (water striders: Veliidae), indicating low-medium preference and nondependence on *Ae. aegypti* as a food source.[96] The capacity and potential of the water scorpion *Nepa cinerea* (Nepidae) as a biocontrol agent of the larvae of *Ae. aegypti*, *Anopheles stephensi*, *Anopheles culicifacies* and *Culex quinquefasciatus* was assessed in laboratory conditions. Although the results were encouraging, *Ae. aegypti* predation rates were lower than for the other mosquito species.[97]

3.2.2.6. Odonata: dragonflies and damselflies. Many laboratory studies have shown odonate nymphs to be voracious predators of mosquito larvae, and in no-choice laboratory situations many Libellulid nymphs will consume *Ae. aegypti* larvae and pupae readily, consuming 133 ± 21 larvae/nymph in 24 h. In containers without further oviposition, complete elimination of all larvae and pupae took 4–9 days depending on stocking density.[98] Other studies are comparative and the effectiveness of five species of immature damselflies and dragonflies (*Anax parthenope*, *Bradinopyga geminate*, *Ischnura forcipata*, *Rhinocypha quadrimaculata* and *Orthetrum Sabina*) was estimated in several water volumes. The nymphs of all species tested were effective predators of *Ae. aegypti* fourth-instar larvae and no effect of water volume (1–3 L) was detected.[99]

These and other studies of predatory efficacy come largely from investigations of biocontrol potential. For instance, the predation efficiency of locally available dragonfly nymphs in Sri Lanka was estimated under laboratory feeding of *Ae. aegypti*. *Anax indicus* (Aeshnidae) had the highest predation rate, although *Pantala flavescens* (Libellulidae) combined effective predation with the widest geographical distribution within Sri Lanka.[100] The biocontrol potential of nymphal *Brachythemis contaminata* (Libellulidae) against larvae of *An. stephensi*, *Cx. quinquefasciatus* and *Ae. aegypti* was studied under laboratory conditions. The dragonfly nymph had lowest predation efficacy against *Ae. aegypti*.[101] They have also, with substantial stakeholder enthusiasm, shown their efficacy in suppressing *Ae. aegypti* populations in domestic water storage containers in Rangoon and Myanmar during augmentative release field trials.[98,102]

Dragonfly larvae are polyphagous animal feeders and their realized diet, as revealed by the analysis of fecal pellets, is varied and mediated by many interacting factors, including the relative abundance of different prey in the environment, the size and habits of these prey, and the ease with which they are caught and devoured.[26] In the field, the ecology and life histories of six species of odonates [*Calopteryx maculata* (Calopterygidae), *Boyeria vinosa* (Aeshnidae) *Cordulegaster maculata* (Cordulegastridae), *Gomphus cavillaris*, *Hagenius brevistylus* and *Progomphus obscurus* (Gomphidae)] were studied in Virginia, USA. The diets of all species were broad and all fed on a wide variety of invertebrates, in particular lake flies (Chironomidae), mayflies (Ephemeroptera) and stoneflies (Plecoptera).[103] This underlines that dragonflies and damselflies are broad and versatile predators which can, and do, consume mosquito larvae, but only as small part of a very varied diet. At present the only clear evidence that unmanipulated odonate populations regularly suppress prey populations is the reduction of treehole mosquito larvae by cohabiting pseudostigmatine damselfly larvae.[104,105] The anthropic forms of *Aedes* spp. mosquitoes have a lower probability of encountering odonate larval predators as these do not tend to occur naturally in ephemeral containers.

3.2.2.7. Platyhelminths: flatworms. The most important flatworm (Turbellarian) predators are species of *Mesostoma* that occur in a wide range of habitats and have been observed to kill and utilize mosquito larvae as a food source.[106] These species display a wide variety of predation mechanisms: some produce a kind of mucus that functions as a toxic web to trap and kill passing prey organisms.[107] Others actively search for suitable prey, thus revealing prey selectivity.[106]

Single prey experiments show that a number of *Mesostoma* spp. feed heavily on mosquito larvae, some chironomid (Diptera) larvae and some daphnids (Cladocera) but considerably less on most copepods and ostracods. Prey preference experiments reflect the same trends. Hence, these predation studies suggest that the flatworms, at high densities, should reduce populations of certain prey species and, consequently, influence community structure. Field studies support this prediction. *Mesostoma* spp., at high densities, appear to be important predators of mosquito larvae in shallow aquatic habitats even under conditions where high densities of planktivorous fishes had little impact.[106]

Predation by the planarian *Dugesia tigrina* on *Ae. albopictus* and *Cx. quinquefasciatus* was explored in a laboratory investigation. With 4, 8 and 12 planarians per assay, mortality of *Ae. albopictus* reached 89.1%, 98.8% and 99.6% and that of *Cx. quinquefasciatus* reached 29.4%, 48.0% and 53.0%. The *Cx. quinquefasciatus* larvae responded more rapidly than *Ae. albopictus* to planarian contact, resulting in greater evasion of predator attacks.[108]

Turbellarian flatworms have an important ecological position in ephemeral ponds, as they can produce resting eggs which can survive dry periods.[106] They remain present through periods of drought and revive to hatch within a few days of rainfall, while most other invertebrate predators become effective only later in the hydroperiod of individual pools or even at later phases of rainy seasons. There is little habitat coincidence with the mosquito species considered here.

3.2.3 By vertebrates

3.2.3.1. Amphibia – Anura: frogs, toads and their tadpoles. Tadpoles, the juvenile life stages of both frogs and toads, are primarily herbivores and are rarely accommodated in small containers (<2–3 L of water).[56] A study of the diets of three anuran species frequently found in the urban areas coincident with mosquito vectors found that none of the tadpoles tested had predated on mosquito larvae and that some species do not have predation-effective mouthparts.[109]

A few species are known to eat insects or even other tadpoles.[110] In North America, the spadefoot toad, green treefrog and giant treefrog all eat mosquito larvae as tadpoles as part of a generalist omnivorous diet.[51] This omnivory has also been demonstrated in other parts of the world with the European green toad, the sandpaper frog, the Indian bullfrog and the coronated treefrog species all recorded as mosquito eaters.[110–112] More specifically, *Ramanella obscura* (Microphylidae) tadpoles have been shown to predate on *Ae. aegypti* larvae.[113] A study of *Rana tigrine* (now *Hoplobatrachus tigerinus*, Dicroglossidae) tadpoles and *Culex fatigans* indicated mass-dependent predation with prey size relating positively to the body weight of the predator. The *R. tigrine* tadpole is also thought to be a more efficient pupal predator than other mosquito predators.[114] Whilst seeking to determine their efficacity as predators of larval, peri-domestic mosquitoes, tadpoles of the Cuban tree frog, *Hyla septentrionalis* (Hylidae), were observed to be cannibalistic, eating egg masses of their own species as well as a variety of material of both plant and animal origin.[115] There are varying degrees of predation observed from species to species and many are truly omnivorous. They are, however, generally considered to have small impacts on larval populations of mosquitoes.[56]

3.2.3.2. Amphibia – Urodela: newts and salamanders. The Salamandridae, in particular the newts (subfamily Pleurodelinae) with their semi-aquatic lifestyle, have also been noted to consume mosquito larvae in the wild.[116] Laboratory assays have demonstrated that the tiger salamander *Ambystoma tigrinu*m (Abystomatidae) readily consume mosquito larvae, including those of *Aedes* spp., and display density-dependent responses to a variety of prey items firmly indicating a generalist and flexible diet. The gut contents of 26% of the wild-caught salamanders used in these studies were found to contain larval and pupal mosquitoes.[117] Also in laboratory assays, larval mole salamanders, *Ambystoma talpoideum* (Abystomatidae) and adult red-spotted newts, *Notophthalmus viridescens viridescens* (Salamandridae) consumed on average 439 $\pm$ 20 and 316 $\pm$ 35 SE third-instar larvae of *Cx. pipiens* per day under conditions of no prey choice.[118]

The larval habitats of the anthropic form of *Ae. aegypti* are unlikely to coincide with newt and salamander habitat, although *Ae. albopictus* may incur some predation by Urodelans at lake edges and wetland habitats. A study of mosquito predators in the Rhine Valley of Germany found that mosquitoes made up only 0.16% of the content of wild-caught newts, indicating that in some natural systems this may be an occasional interaction.[16]

3.2.3.3. Aves: birds. Many birds make use of freshwater habitats and will eat mosquitoes as part of a partially or totally insectivorous diet. Many waterfowl, such as dabbling ducks, are omnivorous and mosquito larvae are a likely part of their diet. There is very little evidence of consumption of *Aedes* spp. in these diets, although martins, swallows (Hirundinidae), waterfowl (Anseriformes: geese, terns, ducks) and migratory songbirds (many taxa) are thought to consume both the adult and aquatic stages of mosquitoes in both simple and complex water bodies.[119,120] In particular, green sandpipers *Tringa ochropus* (Scolopacidae) took mosquito larvae from an Ethiopian sewage lagoon within their winter range. A wide range of other prey were taken with differences reflecting the range of habitats in which the birds were feeding.[120] Predation by birds is considered more fully in the adult mosquito section.

3.2.3.4. Osteichthyes: bony fish. Many fish species have been proposed as control agents for many mosquito species.[12] They are mostly present in permanent water bodies, but can be artificially introduced to temporary ones for ornamental or practical purposes and Chinese health authorities have used several fish species to reduce *Ae. aegypti* larval development in large cisterns or other containers of drinking water. Small fish, such as *Claris fuscus* (the Hong Kong catfish), *Tilapia nilotica* (the Nile tilapia) and *Macropodus* sp. (Paradise fish), have been used in many regions to eliminate larvae in domestic water containers with considerable success; catfish appear particularly effective.[121]

Mosquitofish (*Gambusia* spp.) have been transported and introduced to many areas of the world as mosquito control agents, but studies conducted in natural water bodies do not identify substantial quantities of larval mosquito in their diet. These omnivorous species display dietary flexibility in time and space. For instance, in Hungary investigations recorded 34% algae and 19% detritus with the remaining 47% animal in the gut content

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of *G. holbrooki*; another study of the same species, this time in Spain, found that the animal portion was composed of 11% rotifers, 28% dipterans, 19% ostracods, 19% other insects, 18% copepods and 5% Cladocera.[122] In India *G. holbrooki* favored cladocerans, although copepods and insects also formed a significant proportion of its diet. Mosquito larvae, however, constituted a negligible proportion of its diet.[123]

The guppy *Poecilia reticulata* (Poeciliidae) was observed preying on the larvae of three species of mosquito: *Ae albopictus*, *Ae. aegypti* and *Cx quinquefasciatus*. In this laboratory setting, they favored *Ae. aegypti* over *Ae. albopictus*, and the least preferred was *Cx. quinquefasciatus*.[124] Fish evaluated as effective predators of *Ae. aegypti* larvae in laboratory conditions include *Trichogaster trichopteros*, *Betta splendens* (Osphronemidae), *Astyanax fasciatus* (Characidae), *Poecilia sphenops* and *P. reticulata*. Here, only male *P. reticulata* were less effective and did not consume the total number of *Ae. aegypti* larvae considered typical of a larval habitat under natural conditions.[125]

The oscar *Astronotus ocellatus* (Cichlidae) and the paradise fish *Macropodus opercularis* (Anabatidae) were assessed for predacious behavior toward *Ae. fluviatilis* larvae and the schistosomiasis snail host (*Biomphalaria glabrata*, Mollusca; Planorbidae). The oscar, a species native to Brazil, was a very efficient predator of both organisms and the paradise fish, an exotic species to this region, preyed well on immature mosquitoes, but snails and their egg masses were ingested. Given the option, both fish species preferred live to nonliving food.[126]

3.2.3.5. Reptilia – Testudines: turtles. Turtles are aquatic predators and consume a variety of animals, including the larvae of available and diverse mosquito species. The red-eared slider turtle, *Trachemys scripta elegans* (Emydidae), generally thought to be the most voracious mosquito-feeding turtle, prefers larger larvae (third and fourth instars) and pupae, and can consume from 500 to 1000 mosquito larvae per hour with sufficient availability.[127] With some supplementary feeding, turtles have been used as biological control agents of mosquitoes in inaccessible aquatic habitats such as retention ponds and seasonal storm water catch basins.[128] Keeping one turtle per water-storage tank during field trials for a dengue-control project in Honduras eliminated all mosquito production from this source, and in Louisiana keeping turtles in residential roadside ditches polluted by septic-tank effluent reduced *Cx. quinquefasciatus* larvae and pupae by more than 99%.[127,129] Using this species in biocontrol is now viewed with some caution as it is recorded as one of the 100 most invasive species by the IUCN.[130]

The North American native snapping turtles, *Chelydra serpentina* (Chelydridae), and midland painted turtles, *Chrysemys picta marginata* (Emydidae), have also been recorded eating *Culex* spp. larvae when young turtles were found swimming and hiding among detritus in shallow pools (2–6 cm deep) in Ontario.[127,131] As with other taxa, it is likely that these polyphagous predators do eat mosquitoes in the wild, but are not dependent on them or likely to coincide naturally with the anthropic forms of *Aedes* spp. vectors.

3.3 Adult predation

3.3.1 By invertebrates

3.3.1.1. Arachnida – Aranae and Opiliones: spiders and harvestmen. There is only one known herbivorous spider, *Bagheera kiplingi* (Salticidae), with the rest being predators of insects, other spiders and sometimes small vertebrates.[132] The principal opportunities for spider predation of adult mosquitoes are at emergence from the pupal phase, when resting on vegetation or in houses and, sometimes, directly from flight by web spinners.

Predation by spiders of emerging adult mosquitos has been reported from artificial containers, permanent freshwater bodies and tree-holes. The orb-weaver *Meta* (*Metellina*) *segmentata* (Tetragnathidae) predated on *Culex* spp. emerging from permanent freshwater ponds (7/38) and artificial containers (1/4),[133] and *Meta mengai* caught emerging or ovipositing *Ae. geniculatus* that had flown into a web constructed across a tree hole.[134] Another tree-hole associated spider *Anyphaena accentuata* (Anyphaenidae), however, showed no evidence of predation in this study. Onyeka also reported predation on *Culex* spp. emerging from ponds by *Pirata piscatorius* (Lycosidae) (3/17) and *Theridion ovatum* (Theridiidae) (1/10).[133]

In the squatter areas of Kuala Lumpur, Malaysia predators of *Ae. aegypti* were identified serologically using the precipitin test. Gut smears from 230 spiders caught in houses found that five species of spider produced positive reactions, *Araneus* (*Neoscona*) *theisi* (78/150), *Araneus* sp. (14/24), *Neoscona* sp. (Araeneidae) (10/38), *Plexippus petersi* (3/10) and *Plexippus paykulli* (Salticidae) (3/7), and are considered to be natural predators of *Ae. aegypti*.[135] The rubber estates around Kuala Lumpur were also surveyed for natural predators of *Ae. albopictus*, again identified by a precipitin test. The extracts of 248 gut smears on filter paper of various invertebrates, mainly spiders, gave positive reactions in the trashline orb-weaver *Cyclosa insulana* (5/18), *Nephila maculate* (6/18) (Araneidae), the huntsman *Heteropoda venatoria* (Sparassidae) (9/10), the orb-weaver *Leucauge grata* (Tetragnathidae) (18/39) and the wolf spider *Passiena* sp. (Lycosidae) (41/98).[136] More recently, up to 90% of the gathered spiders from rubber plantations and a cemetery in Malaysia were identified as feeding on Asian tiger mosquitoes.[61]

Jumping spiders (Salticidae) in both Africa and South-East Asia do feed on mosquitoes as part of diverse diets and in Africa have shown preference for recently blood-fed mosquitoes.[61,137,138] Laboratory observations of *Crossopriza lyoni* (Pholcidae) spiderlings revealed that after first molting, they were capable of throwing silk to capture and overpower *Ae. aegypti* many times their size, and of storing individuals for up to 6 days until ready to feed.[139] With limited prey choice the major part of the diet of these spiders, however, was not mosquitoes; cannibalism accounted for 67–84% of spider mortality in their caged replicates.

In the UK, 645 gut smears from arachnids caught by sweep-netting vegetation in habitats at Monks wood, Ham Street wood and Arne in Dorset found that 30/121 of spiders were positive, suggesting that spiders are important predators of mosquitoes resting in vegetation.[57] This work also reported that a high proportion of Opiliones gave a positive reaction, but few (36) were tested and little is known of their mosquito consumption.

In another context, *Theridion* (*Nesticodes*) *rufipes* (Theridiidae) was found in rearing cages of *Ae. aegypti* in the School of Medicine, San Juan, PR. From the 1970s to the 1990s, the spiders were long-term residents and a single spider eventually could eliminate all the mosquitoes in a cage.[140] It is evident that spiders will eat mosquitoes and that many do eat *Aedes* spp. They are, however, generalist opportunistic predators with little prey specificity when it comes to mosquitoes.

3.3.1.2. Diptera: flies. In the south of England, predaceous Diptera appeared to be important predators of emerging adult

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mosquitoes,[57] with relatively large populations of these flies and a high incidence (25–28%) of feeding on emerging *Ae. cantans* (and possibly on ovipositing females). Five species of dagger fly (Empididae), three long-legged flies (Dolichopodidae), a dung fly (Scatophagidae) and a scavenger fly (Anthomyiidae) between them were considered, probably, to cause a greater population loss (estimated at 13–14% of all emergent *Ae. cantans*) at this vulnerable moment than any dipteran predation on the immature stages.[57] Shore flies (Ephydridae) have been reported to eat anopheline mosquitoes and with the phantom midges (Chaoboridae) also known to eat mosquito larvae are likely to consume *Aedes* spp. on occasion, but there is no evidence linking these generalist species to the *Aedes* spp. considered here specifically.

3.3.1.3. Mantodea: mantids. The mantises are distributed throughout the world and are mostly sit-and-wait ambush predators with a range of invertebrate and vertebrate prey.[141] A small cage study of *Hymenopus coronatus* and *Phyllocrania paradoxa* provides evidence of *Aedes* spp. mosquito consumption, but offers no indication of potential field levels or dietary proportion.[142]

3.3.1.4. Odonata: dragonflies and damselflies. There is a long history of dragonflies being considered as substantial consumers of adult mosquitoes[104] and while there is anecdotal evidence, there is no quantified published field evidence to support this. Dragonflies can find and forage in dense swarms of mosquitoes, but it is unlikely they can affect numbers of mosquitoes at a population scale or that they depend on mosquitoes as a food source.[143,144] Adult Odonata are effective and flexible generalist predators and, principally, tend to feed on the most abundant and available prey.[104] Specific evidence of *Aedes* spp. consumption or any hint of dependence was not found.

3.3.2 By vertebrates

3.3.2.1. Amphibia – Anura: frogs and toads; Urodela: newts and salamanders. As adults, many species of both Anurans and Urodelans are largely insectivorous. Their interactions with adult mosquitoes are little known and unlikely to be sufficient for population-level effects or for any strong ecological link to be asserted.[145] It is most likely that some smaller frog and salamander species do take resting *Aedes* spp. adults opportunistically from vegetation, but no quantification of this was identified in this review.

3.3.2.2. Aves: birds. Many species of insectivorous birds are observed to eat mosquitoes and their prey choice is observed to be largely positively density dependent; they will eat these most when they are most abundant.[146] The most common adult mosquito-eating birds are swallows, martins, warblers and sparrows. Many of the studies available to describe this predator–prey interaction are based in wetlands and reflect the diverse and complex ecologies of these sites as well as the mosquito controls that may be applied there.[119,147,148] The studies and reviews available support that insectivorous birds generally have diverse diets and while they may consume mosquitoes broadly, these are a small portion of their diet and this shifts readily to other invertebrates if control operations reduce mosquito availability.[12,148,149]

Some detail is available on the diet of the purple martin, *Progne subis* (Passeriformes: Hirundinidae), as this has been anecdotally framed as a voracious consumer of mosquitoes. The Purple Martin Conservation Association explored this and concluded that various mechanisms coalesce so that mosquitoes form only a small part of the overall diet of the birds.[150] For this and many other insectivorous birds, differences in flight timing, flight height and location, and the mosquitoes' small size result in them being minor diet items. The American Mosquito Control Association states that 'The number of mosquitoes that martins eat is insignificant' and in-depth studies have shown that mosquitoes make up approximately 0–3% of the diet of martins.[151]

Other work supports this 'small component' conclusion and indicates that birds tend toward larger, more rewarding prey. For example, the diet of the barn swallow *Hirundo rustica* (Passeriformes: Hirundinidae) in Ontario was studied using DNA metabarcoding. This revealed that mosquitoes were not in the top five taxa consumed despite six species of *Aedes* being found among the four mosquito genera found in malaise traps at their study sites. Birds were observed to be biased towards large prey items and altered with prey availability.[152]

Mosquito control studies do report ecological consequence to applications of *Bacillus thuringiensis* var. *israelensis* (Bti), a naturally occurring soil bacterium used in the biological control of some Nematocera (a Dipteran suborder that includes midges and mosquitoes) with biomass being reduced by 50–83% in the second and third years of treatment at wetland sites in Minnesota, although direct effects on the bird community could not be inferred.[119] The lack of close coupling seen between dipteran biomass and breeding bird abundance and nesting success may reflect the scale and ecological complexity of these wetlands, such as the presence of other limiting factors on population distribution and abundance. In the Camargue area of southern France a similar study found nesting success and fledgling survival of the house martin *Delichon urbicum* (Passeriformes: Hirundinidae) were lower at treated sites relative to control sites (2.3 *versus* 3.2 chicks produced per nest). Intake of Nematocera and their predators (spiders and dragonflies) decreased at treated sites, and was compensated for by increased consumption of flying ants.[148] The ecological consequence of using a mid-breadth bio-pesticide noted here has little inference for the specific control of individual species as Bti acts on a taxonomic range of much greater breadth. As part of another study into the ecological consequence of Bti, the food selection of *D. urbicum* in the upper Rhine Valley, Germany, was investigated with neck ring samples. This largely consisted of diurnal insects with terrestrial larvae (Aphidina, Brachycera, Coleoptera) and mosquitoes were consumed, although not preferred.[149]

The importance of 13 taxa in the house wren, *Troglodytes aedon* (Passeriformes, Troglodytidae), diet was tightly correlated to their biomass available. This was largely true within taxa also as when larger individuals within a taxa were available they were consumed in greater proportion by wrens. Chironomids (nonbiting midges) were an exception and small individuals were consumed in greater proportion than expected from their background abundance. Prey selection was concluded to depend on abundance, size and ease of capture.[153] The western bluebird, *Sialia mexicana* (Passeriformes, Turdidae), diet was studied using molecular methods and high-throughput sequencing. They consumed a broad diet comprising 66 arthropod species from six orders and 28 families. In this species, evidence of *Aedes* spp. consumption was high and found in 49.5% of the fecal samples.[154]

Insectivorous birds are predators in many ecosystems and forage flexibly on small taxa, but there are no recorded mosquito-specialist predators.[12,147]

3.3.2.3. Mammalia – Primata: bats. Insectivorous bats are often considered to be important predators of mosquitoes, although this is unlikely for the mosquito species considered here as there is temporal separation between their diurnal habits and the crepuscular and nocturnal hunting of bats. Of the four general foraging strategies used by bats, aerial hawking (catch on the wing) and gleaning (take from vegetation or ground) bats are most likely to consume mosquitoes. Larger bats tend to use low-frequency echolocation to detect higher-value, larger prey, and the longer wavelength of this echolocation is unsuitable for detecting small prey such as mosquitoes.[155]

An investigation of the natural prey of two free-tailed bat species, *Chaerephon pumilus* and *Mops condylurus* (Chiroptera, Molossidae), using PCR amplified from fecal pellets found Lepidoptera and Diptera were widely present among the samples analyzed. The two families most frequently identified were the Noctuidae and Nymphalidae (Lepidoptera), suggesting that moths dominate their diet.[156] Another study of five eastern Australian bat species which looked specifically for evidence of *Aedes* spp. consumption identified this in the two smallest species (<5 g), *Vespadelus vulturnus* and *Vespadelus pumilus* (Chiroptera, Verspertilionidae), despite locally abundant *Aedes* species. They concluded that mosquitoes were not always available to bats and therefore only make up a small fraction of their diet due to their small size, poor detectability by low frequency echolocation and variable field metabolic rates.[157] Mosquitoes were rare in feces of *V. pumilus*, but present in 55% of feces of *V. vulturnus* individuals. The authors calculated that to meet nightly energetic requirements, *Vespadelus* spp. would need to consume ~600–660 mosquitoes on a mosquito-only diet or ~160–180 similar sized moths on a moth-only diet. The lower relative profitability of mosquitoes may explain low mosquito consumption among these bats and the absence of mosquitoes in feces of larger bats.[157] For smaller bats foraging in natural systems there may though be a habitat-use response to mosquito prey availability. Radio-tracked *V. vulturnus* varied its foraging range in correspondence with a spatio-temporal variation in abundance of *Ae. vigilax*, which may reflect the importance of mosquitoes as a dietary item in this context.[158]

The free-tailed bats, *C. pumilus* and *M. condylurus*, were also studied in Swaziland, concluding that they are dietary generalists and, although mosquitoes were part of the diet, lepidopterans make up the majority.[156] Diet analyses using similar techniques of other chiropteran species echo these patterns of bats as opportunistic and size-dependent feeders: the little brown bat, *Myotis lucifugus* (Chiroptera, Verspertilionidae), ate 71% small moths, 16.8% spiders and 1.8% mosquitoes while the big brown bat, *Eptesicus fuscus* (Chiroptera, Verspertilionidae), ate mostly beetles and caddisflies.[159,160] Similar was found for these species in a different part of their range in Wisconsin, USA.[161] A recent study using metabarcoding of bat fecal DNA in Belize echoes this insectivorous generalism, with dipterans making up a small proportion of the diet of insectivorous bats, and within the dipterans few were found to be Culicidae.[162]

A dietary study of four species of urban-roosting bats in three Brazilian cities is particularly pertinent and indicates that the bats forage largely on agricultural pests in areas just outside the city. Of the five species for which fecal samples were barcoded, three, *Nyctinomops laticaudatus*, *Molossus molossus* and *Eumops perotis*, were found to have consumed Culicidae in a total of 6/43 samples sequenced.[163] Thus, despite being proposed as suitable biological control for mosquito populations, there is substantial evidence that mosquitoes represent only a small proportion of the diet of most bats and that other insects, such as moths, provide better nutritional value.

3.3.2.4. Reptilia – Squamata: geckoes and lizards. Some terrestrial reptiles do consume adult mosquitoes and although there is little published quantification there is much anecdotal observation of geckoes and lizards hunting around houses during the day and around their lights at night in the peri-urban areas of many parts of the world.[164,165]

A small-cage study of two gecko species, *Phelsuma standingi* and *Phelsuma laticauda*, demonstrated both species will feed on *Aedes* spp., with *P. standingi* consuming more mosquitoes and showing some preference for *Ae. arabiensis* compared to *P. laticauda*.[142] In an experimental study in laboratory conditions the Australian dubious dtella gecko *Gehyra dubia* and the exotic Asian common house gecko *Hemidactylus frenatus* (Squamata, Gekkonidae) both consumed *Ae. aegypti* in a positively density-dependent way and both favored female mosquitoes over males even when not blood-fed. In a seminatural setting (32 m^3 study room) *G. dubia*'s predation rates on various Australian mosquito species varied. Five photophilic mosquito species (*Ae. vigilax*, *Anopheles annulipes*, *Coquillettidia xanthogaster*, *Culex annulirostris* and *Culex sitiens*) suffered 78–100% predation, compared with 33–53% predation of four nonphotophilic species (*Ae. aegypti*, *Ae. notoscriptus*, *Ae. vittiger* and *Cx. Quinquefasciatus*). When offered a mixture of unfed, freshly blood-fed and gravid females of *Ae. aegypti* in an illuminated terrarium, both gecko species consumed more unfed than fed or gravid female mosquitoes, possibly because the unfed mosquitoes were more active.[166]

Field observations in Thailand of over 1000 attacks by the common house geckoes *H. frenatus* and *Hemidactylus platyurus* found that 36% of the attacks were on Diptera, but that Culicidae amounted to 3% and 5% of these species respective foraging incidences.[164] Structural equation models based on observations of food-web component abundances do suggest that house geckoes and spiders are important predators of *Aedes* spp., but that in urban landscapes the consumption of spiders by geckoes may reduce overall predation.[167]

4 SUMMARY OF FINDINGS

4.1 Predation of eggs

Other mosquitoes, backswimmers, ants, beetles, cockroaches, pill-bugs, dragonflies and earwigs have all been reported to consume *Aedes* or related-species' eggs. The same was found for juvenile salamanders, frogs and toads as well as fish. Many of these preference studies have, however, been in enclosed, simplified systems and should not be overly extrapolated. In contrast, predators of *Ae. cantans* were studied at four locations in southern England using a precipitin test. The gut contents of 2893 recently fed predators were tested and no egg predators were found.[57] 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. The animals found to consume mosquito eggs are all generalist predators and not reliant on a single species of mosquito as food source, and there is now some evidence that, for some invertebrate taxa at least, *Aedes* spp. eggs may be a sub-optimal or incomplete diet.[48]

Table 1. Summary of the identified invertebrate predators of egg, larval and adult life stages of the mosquitoes *Aedes aegypti* and *Aedes albopictus*

Predator Order	Egg	Larva/ pupa	Adult
Arachnida - Aranae, Acari & Opiliones (spiders, mites and harvestmen)		Many peri- and semi-aquatic spiders feed on mosquito larvae, though there is no evidence of any *Aedes* specialisation. Aquatic mites also infest mosquito species, but no dependence or specialism has been suggested.	Many spiders and harvestmen are opportunistic predators of emerging adults or those resting on vegetation. Some orb weavers do catch *Aedes Spp.* in flight and may weave over the mouths of tree holes in nature. No specialisation is evident.
Blattodea (cockroaches)	The American cockroach can cause substantial egg loss at surface sites.		
Coleoptera (beetles)	Lady beetles will consume eggs, but cannot complete their larval development on these exclusively	Dytiscid diving beetles consume Aedes Spp. larvae and can reduce their numbers substantially if introduced to containers. In established water bodies mosquitoes represent a small proportion of their diet.	
Crustacea		Many copepods, triops and freshwater shrimp are widely distributed, resilient and consume *Aedes Spp.* larvae voraciously in laboratory experiments. Their diverse field diets indicate no dependence on these mosquito species.	
Dermaptera (earwigs)	Earwigs will consume eggs in field investigations		
Diptera (flies)	Larvae of other mosquito species (*Toxorhynchites Spp.*) willl eat eggs opportunistically, but favour larvae	Mosquito larvae found to make-up 5-6% of the diet of predatory mosquito (*Toxorhynchites Spp.*) larvae in tree holes and tyres.	Shore flies and other diptera predate emerging adults at the air-water interface and can consume substantial numbers of emerging adults in natural settings.
Hemiptera (true bugs)	Notonectid backswimmers destry and sink egg rafts in mesocosm experiments	Several families (Corixidae, Belostomatidae, Velidae and Nepidae) are known to consume mosquito larvae. No feld studies suggest preference for, or dependence on *Aedes Spp.* larvae	
Hymenoptera (ants)	Several ant species are recorded as predating eggs in laboratory and field situations		
Isopoda (woodlice / pill bugs)	Pill bugs will consume eggs in field investigations		
Mantodea (mantises)			A small cage study demonstrates consumption. No field evidence.
Mollusca - Gastropoda (snails)		A species of pond snail was recorded to consume radio-tagged *Aedes Spp.* larvae.	
Odonata (dragonflies and damselflies)	Dragon flies will consume eggs, but prefer alternate prey	Dragonflies and damselflies do consume *Aedes* larvae, but their natural diet is broad and flexible.	Adult Odonata are effective and flexible generalist predators and, principally, tend to feed on the most abundant available prey
Platyhelminths (flatworms)		Turbellarian flatworms are well-adapted to ephemeral aquatic situations and include mosquito larvae as part of their wide and opportunistic diet.	
Psocoptera (booklice and bark lice)	An identified egg predator in an insectary context		
Trichoptera (caddis flies)		A limnephilid caddis fly was recorded to consume radio-tagged *Aedes Spp.* larvae in ephemeral water bodies	
Summary Comment	**All species identified are generalist, opportunistic predators of mosquito eggs**	**All species identified are generalist, opportunistic predators of mosquito larvae**	**All species identified are generalist, opportunistic predators of adult mosquitoes**

Table 2. Summary of the identified vertebrate predators of egg, larval and adult life stages of the mosquitoes *Aedes aegypti* and *Aedes albopictus*

Predator group	Egg	Larva/ pupa	Adult
Amphibia - Anura (frogs & toads) and Urodela (salamanders & newts)	Tadpoles of frogs have been experimentally demonstrated to eat eggs, though predation by newts was rare even in situations of no choice.	Some species of anurans (frogs and toads) and urodelans (salamanders & newts) in either, or both, juvenile and adult life stages eat mosquito larvae. They can be voracious in confined situations, though none have displayed any specialism on mosquitoes which are both inconsistently eaten and a small portion of their diet.	Occasional capture is likely, but no quantitative evidence or strong ecological link emerged from the literature
Aves (birds)		Martins, swallows (Hirundinidae), waterfowl (Anseriformes: geese, terns, ducks) and migratory songbirds (many taxa) are thought to consume the aquatic stages of mosquitoes in both simple and complex water bodies. There is no evidence of abundant consumption of *Aedes Spp.*	Many species of insectivorous birds eat mosquitoes in a density dependent manner. The most common adult mosquito-eating birds are swallows, martins, warblers and sparrows. Evidence of *Aedes Spp.* consumption was found in the fecal matter of 49.5% of the western bluebird.
Mamalia - Chiroptera (bats)			The smaller insectivorous bats are predators of mosquitoes, though the *Aedes Spp.* considered have some temporal separation between their diurnal habits and the crepuscular and nocturnal hunting of bats. Mosquitoes make-up very small portions of the diets of most bats, though this can rise in time and space. In one study mosquitoes were detected in the fecal samples of 55% of *Vespadelus vulturnus.*
Osteichthyes (bony fish)	Mesocosm experiments indicate fish may consume egg rafts. These *Aedes Spp.* do not raft their eggs.	Many fish eat mosquito larvae as part of their varied diet in natural ecosystems. Several species are useful in controlling *Aedes Spp.* larvae in human-associated water storage containers, though need artificial introduction.	
Reptilia - Testudines (turtles) and Squamata (geckoes & lizards)		Turtles are polyphagous aquatic predators do eat substantial numbers of mosquitoes in the wild, but are not dependent on them or likely to coincide naturally with the anthropic forms of *Aedes Spp.* vectors.	Some geckoes and lizards do consume adult mosquitoes but there is little published quantification. There is observation of these hunting around houses and their night lights in the peri-urban areas of most parts of the world.
Summary Comment	**All species identified are generalist, opportunistic predators of mosquito eggs**	**All species identified are generalist, opportunistic predators of mosquito larvae**	**All species identified are generalist, opportunistic predators of adult mosquitoes**

4.2 Predation of larvae and pupae

Many taxa contain predatory species which consume mosquito larvae as this is the stage which has the most predictably located, easily captured and abundant biomass. Despite this, none of the predator species identified here rely in any great part on the larval and pupal stages of *Aedes* spp. The seasonal pattern of availability of this larval resource itself encourages a diverse diet and all predators identified here are regarded as polyphagous and nondependent on mosquito larvae of any genus. Many published studies of the predators of *Aedes* spp. mosquito larvae aim to identify and evaluate potential biocontrol agents. The selection of biological control agents relies in part on their self-replicating capacity, their preference for the target pest in the presence of alternate natural prey and environmental adaptability to the habitat or location. Many of the candidates thought of as promising in mosquito control are not suitable in the majority of urban and peri-urban environments exploited by the larvae of the anthropic forms of the *Aedes* species we consider specifically here.[168]

4.3 Predation of adults

Many invertebrate and vertebrate taxa contain predatory species which consume mosquito adults. The dispersion and mobility of this disaggregated resource itself ecologically discourages any dependence or a narrow (stenophagic) diet. All predators identified here are regarded as polyphagous, opportunistic and nondependent on mosquito adults of any genus (Tables 1 and 2).

5 CONCLUSION

Ae. aegypti and *Ae. albopictus* are important mosquito species which interact closely with people in and around urban and suburban areas. They vector devastating diseases and the human and economic consequences of these makes it vital to understand (i) the role of natural predators in their population suppression and (ii) the influence that successful population suppression through vector control operations might have on animals which consume them. Both species have anthropic and wild-type forms; these latter take their blood meals principally from other vertebrates and form a part of diverse prey communities. Of principal consideration for this review have been the predatory relationships on the anthropic forms which exist in a different habitat and context to those where most 'natural' predator studies take place. We can infer many things, with some caution, from wider studies, although many of the predators which consume these *Aedes* spp. in those ecotypes are unlikely to be present in influential numbers in the human-associated environment. When living near people, these anthropic invasive mosquitoes are also frequently subject to other control methods such as insecticide treatment, insect growth regulator application and source reduction, it is ecologically and theoretically highly unlikely that any predator would depend on them.

No literature has been identified which either proposes or demonstrates that any plant, invertebrate or vertebrate predator was found to depend on on *Ae. aegypti* or *Ae. albopictus* as a vital or important food source. Mosquito species are most important as prey in their aquatic larval habitats but are a seasonal and often ephemeral item there. Because the anthropic forms of the species considered here usually use man-made containers such as gutters, water containers, cans and tires as larval habitat, the predators that do occur are generalist and opportunistic, and feed on larvae if and when they encounter them. Although some adult mosquitoes are foraged from swarms and captured by spiders' webs and mantids, they are generally a low-value, disaggregated and mobile food item when flying. *Aedes* spp. adult mosquitoes may be more vulnerable to predation when resting than flying and in the urban landscape may benefit from human hygiene which suppresses many potential predators. Some potential generalist predators of adult mosquitoes, such as geckoes and frogs, are sometimes welcomed and encouraged by people, although these often have a spatial or temporal disconnect which reduces their mosquito-consuming capacity and thus any ecological linkage.

The studies identified by this extensive review come together to suggest little potential risk of the adverse impact of suppressing or eliminating invasive *Aedes* spp. on predators and food webs. This conclusion, however, should be viewed with some caution as the majority of the cited studies arose from ecological- or biological-control investigations and did not intend to test this hypothesis. Spielman's[169] comment that these mosquitoes are of no ecological benefit may thus not apply to natural systems. In the anthropic-dominated environment of urban and peri-urban areas it seems unlikely that species-focused vector controls such as SIT, IIT or genetic strategies would affect the opportunistic interacting species adversely.

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TC and JB conceived the article and received support from L-CG. JB and TC contributed equally to the work and wrote the original manuscript. All authors commented and gave final approval for publication.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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