Special Collection: 2020 Highlights of Medical, Urban, and Veterinary Entomology

Highlights of Medical Entomology, 2020

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Abstract

Medical Entomology as a field is inherently global – thriving on international and interdisciplinary collaborations and affected dramatically by arthropod and pathogen invasions and introductions. This past year also will be remembered as the year in which the SARS-CoV-2 COVID-19 pandemic affected every part of our lives and professional activities and impacted (or changed, sometimes in good ways) our ability to collaborate and detect or respond to invasions. This incredible year is the backdrop for the 2020 Highlights in Medical Entomology. This article highlights the broad scope of approaches and disciplines represented in the 2020 published literature, ranging from sensory and chemical ecology, population genetics, impacts of human-mediated environmental change on vector ecology, life history and the evolution of vector behaviors, to the latest developments in vector surveillance and control.

Key words: medical entomology, invasion biology, behavior, control

The 2020 Annual Meeting of the Entomological Society of America and the Medical, Urban, and Veterinary Entomology section meetings were held virtually as a consequence of the ongoing SARS-CoV-2 pandemic. The effects of the pandemic on our field have been profound and will likely play out for years to come, as a result of demands on public health stakeholders’ time (and in some cases, funding) being diverted to the COVID-19 response, and the broader implications of the impact on researcher’s wellbeing and time. Reduced ability to continue with laboratory and fieldwork will affect research output in coming years, potentially with a shift to reviews and other types of analytical publications that are more conducive to working-from-home. Due to demands on the health care system, it is also possible that reported case numbers of vector-borne diseases will appear to dip. Repercussions of people spending more time in and around their home due to stay-at-home orders on vector-borne disease transmission are still unclear. Studies that have reported effects of lockdowns on dengue transmission appear to be quite variable (Brady and Wilder-Smith 2021). Control and elimination programs of vector-borne diseases will be affected to varying extents (Toor et al. 2021). In other words, challenges to medical entomology have only become more pronounced.

It appears especially worthwhile then to survey our field in 2020, with much of the output reflecting research projects that were started before the pandemic, and highlight a subset of publications that represent particularly exciting steps forward. This article is by no means exhaustive or comprehensive, and is strongly biased toward papers I personally thought were exciting, elegant, and noteworthy. The screening of articles was likewise not systematic. Although for certain journals (e.g., the Journal of Medical Entomology) the table of contents of each issue were inspected, many other articles were discovered via regular reading or social media. Articles were selected that either appeared in print in final form in 2020, or that became available online that year, following peer-review and acceptance (although the final citation may be published in 2021).

The highlighted articles fit within themes of ticks and tick-borne diseases, from surveillance to understanding environmental determinants of range expansions; biology and genetics of invasive Aedes species; mosquito host choice and feeding behavior; effects of vector diversity on pathogen transmission; novel vector control approaches; and studies highlighting impacts of human-mediated environmental change on vector behavior and vectorial capacity.

Ticks and Tick-Borne Diseases: Environmental Determinants of Range Expansions

Both the number of tick-borne pathogens known to infect and cause morbidity in humans and the overall number of tick-borne disease cases in humans are steadily rising. Expanding ranges of...
mediated by different tick species. The authors found that areas associated with low- and medium-level risk of active spread are found in coastal and low-lying areas, whereas areas with high-risk potential are found in mountainous and rural areas.

Invasion Biology and Genetics of *Aedes* spp.

One of the most important arbovirus vectors globally, *Aedes aegypti*, L. (Diptera: Culicidae) is thought to have originated in continental Africa. A new study by Soghigian et al. (2020) explored the evolutionary relationship of populations of *Aedes aegypti* and *Aedes aegypti* (populations from outside Africa) to *aegypti* group species found in islands of the Indian Ocean. This analysis suggests that an ancestral *Stegomyia* lineage diversified in the Indian Ocean islands around 16 million years ago, and that this group was basal and gave rise to *Ae. aegypti* in continental Africa (Soghigian et al. 2020).

Further insights into the evolution of anthropophagic behavior in *Ae. aegypti* came from a study that investigated the host choice of this species for humans versus other animal odors and tied this to environmental factors at the 27 sites in sub-Saharan Africa from which populations were assessed. The majority of the variation in host preference was related to the intensity of the dry season and, to a lesser extent, human population density, pointing to a reliance on water storage by humans in strongly seasonal environments as a potential selective force behind anthropophily in this species (Rose et al. 2020).

An important question for invasive mosquitoes is whether and how their vector competence and other traits related to vectorial capacity change due to genetic changes during the invasion process. This topic was explored for *Aedes albopictus* (Skuse) populations from various continents, including their center of origin. Six distinct lineages were identified and tested for dissemination and transmission efficiency of the chikungunya virus. Two of these lineages, that were dominant in La Reunion and the Mediterranean region, showed greater levels of vector competence, highlighting that in newly invaded areas, the public health outcomes may be affected by the source of origin (Vega-Rúa et al. 2020). Gains also continued to be made in our understanding of the environmental and land use factors driving receptivity for invasion. In a study making use of data from 338 trap sites in New York State, the authors found that areas associated with low- and medium-level...
development, as well as low proportions of deciduous cover, were more likely to have increased numbers of *Ae. albopictus*, whereas the effects of precipitation on *Ae. albopictus* abundance was positive at lower levels, but then found to switch to a negative relationship above a threshold of ca. 70 mm during the preceding 28 d, perhaps due to flushing of habitats (Kache et al. 2020).

**Mosquito Feeding Behavior**

Studies of mosquito blood-host preferences and feeding rates and plant-sugar feeding are critically important to understanding both vectorial capacity (VC) and, potentially, for the development and use of control measures that exploit mosquito feeding habits. How the proportion of hosts fed upon affects the vectorial capacity of *Cutella melanura* (Coquillett) for Eastern equine encephalitis virus (EEEV) was investigated by West et al. (2020). They found that spikes in equine cases of EEEV occurred in May and June in Florida, while their estimates of VC were highest from June to August (when abundance peaked). The peak in cases appeared to coincide with the increasing proportions of blood-fed and parous *C. melanura* and host use that included a mix of birds, reptiles, and mammals (West et al. 2020). Whether and how these observed discrepancies were due to this being a zoontic virus, with the possible involvement of additional bridge vectors, is worthy of further study.

Nectar and bloodmeals serve different purposes for mosquitoes, trigger different metabolic pathways, and are shunted to different parts of the digestive tract, yet how mosquitoes tell these meals apart at a sensory level is not well understood, particularly given that glucose is a component of blood. A study using calcium-imaging identified four distinct neuron classes in the stylets of *Ae. aegypti*, which respond to specific components of blood and to glucose only when in the presence of other blood components. Further, these stylet neurons did not respond to nectar-specific sugars (Jove et al. 2020). Likewise, the sensory processing involved in nectar-source seeking remains understudied. This topic was addressed in a study using *Ae. aegypti* and other *Aedes* spp., and the orchid *Platanthera obtusata*, which is visited and pollinated by mosquitoes. *P. obtusata* was found to emit a blend of volatiles that included a pronounced level of nonanal, whereas other closely related orchids which do not elicit visitation by mosquitoes had odor profiles dominated by lilac aldehyde. Using calcium-imaging Lahondere et al. (2020) were able to show that both these volatiles activate antennal lobe glomeruli and that the ratio in which these occur appears to determine attractiveness and allow for discrimination between floral sources. Given the potential to harness mosquito’s nectar-feeding habit for control or surveillance purposes, there is great value in improving our understanding of when, where, and how likely different species are to engage in this behavior. The rate at which *Ae. albopictus* feeds on sugar under field conditions in the northeastern U.S. was investigated. Approximately 42% of female *Ae. albopictus* were fructose positive, and positivity was greater when environmental conditions were dry and in locations where flowering plants were more abundant (Fikrig et al. 2020). Sugar feeding under field conditions by *Culex quinquefasciatus* (Say) and *Ae. aegypti* was investigated in southern Texas (Olson et al. 2020). For *Ae. aegypti*, the sugar content of mosquitoes was greater from autumn collections than for those from the summer, suggesting a seasonal difference in sugar-feeding behavior. Overall approximately 43% of female *Ae. aegypti* were fructose positive, adding to the evidence that in certain environments this species does frequently feed on sugar.

A challenge in medical entomology relates to accurately assessing the demography of natural vector populations. A literature review of survival estimates for field populations cautioned that different methodologies for estimating mosquito survival from field-collected populations can lead to different biases, and sometimes large differences in survival estimates (Matthews et al. 2020). Another enduring question is whether and how infection with pathogens changes mosquito behavior and physiology. One such aspect, how infection changes mosquito behavior when exposed to repellents, was addressed using a systematic review and meta-analysis. Across all studies, the authors found a 62% reduction in repellency attributable to pathogen infection of the vector, but this effect was strongly dependent on several factors, including mosquito age and the pathogen studied. Notably, *Plasmodium* and dengue did not show an effect on repellency, whereas infection with *Edhazandra aedis*, Zika virus, or Sindbis virus did (Lajeunesse et al. 2020).

**Effects of Vector Diversity on Transmission**

The main theoretical underpinnings of medical entomology, from the development and refinement of Ross-Macdonald models to concepts such as vectorial capacity, have their basis in single vector and host systems. Interest is growing in understanding how the transmission ecology of multivector and multihost systems differ, and what these repercussions mean for surveillance and control. Differences among members of species complexes are also being studied. In Chicago, which experiences persistently high West Nile virus transmission, the host selection and genetic makeup of *Culex pipiens* (L.) complex mosquitoes was investigated during July and August in 2012. The vast majority (99%) of bloodmeals in this study came from avian hosts, with both northern cardinals and American robins being bitten more frequently than their abundance would suggest. There was a modest amount of introgression between *Cx. pipiens* f. *pipiens* and f. *molestus*, as well as between *Cx. pipiens* f. *pipiens* and *Cx. quinquefasciatus* (Say), but no evidence was found that hybridizations led to differences in feeding patterns (Kothera et al. 2020). Differences in responses to host volatiles were shown between *Cx. quinquefasciatus* and *Cx. pipiens* molestus in laboratory behavioral assays comparing attraction to headspace volatiles of magpies, chickens, and pigeons, with or without CO2. Although the addition of CO2 to the headspace volatiles led to an increase in responsiveness by *Cx. quinquefasciatus*, this was not the case for *Cx. pipiens molestus*, suggesting these species have developed different host-seeking strategies (Spanoudis et al. 2020). The role of *Culex* species also was investigated in Andalusia, Spain, where both West Nile virus (WNV) and avian malaria are transmitted by *Cx. pipiens*, *Culex perexiguus* Theobald, and *Culex modestus* Ficalbi. The authors developed a multispecies R0 model and used field-collected data to determine species-specific contributions to the transmission that suggested *Cx. perexiguus* was the main driver of WNV transmission in this region, whereas the R0 of *Plasmodium* was higher when *Cx. pipiens* was present in the mosquito community (Ferraguti et al. 2020). A reanalysis of mosquito and malaria surveys from Kilifi, Kenya, assessed various components of vector diversity and how this affected malaria transmission. There was a positive relationship between anopheline species richness and malaria prevalence in humans, and community composition influenced malaria prevalence as well, where a high ratio of *Anopheles arabiensis* Patton to *Anopheles gambiae* Giles led to a decrease in prevalence (Hoi et al. 2020).

**Novel Control Approaches**

The dependency of vector control on approaches that rely on a handful of insecticides has become a liability due to the evolution of insecticide resistance and other constraints. Integrated approaches
that use a wider variety of methods, based on a sound understanding of local ecology and guided by monitoring and evaluation have been promoted as a more sustainable way forward (Wilson et al. 2020). It is also clear that additional, novel methods of control will be needed. A brief overview of some of exciting developments from this past year is described here.

The potential to target the nectar-feeding behavior of mosquitoes for control has received a lot of attention in recent years. Another approach where this behavior could play a role is in microbial forms of control, where nectar-feeding could potentially be a means to transfer bacteria to mosquito populations. Asaia spp. have been investigated for their use in paratransgenesis, the genetic modification of this bacterium to impede the competence of mosquitoes for specific pathogens. A recent study isolated Asaia spp. from plants and mosquitoes in Senegal, and demonstrated that mosquitoes could inoculate flowers with Asaia, and subsequently these plants could transmit the bacterium to mosquitoes through nectar-feeding (Bassene et al. 2020). The use of Wolbachia continues to show promise as a dengue control mechanism. In a field trial performed in Kuala Lumpur, Malaysia, the potential to use the wAlbB strain of Wolbachia for dengue control was investigated. Aedes aegypti carrying this strain were released at 6 sites with endemic dengue, and the persistence of Wolbachia in mosquitoes rose quickly, and remained stable in some sites, while others required additional mosquito releases. Dengue incidence was estimated to decrease by approximately 40% following the releases (Nazni et al. 2019). A newly detected vertically-transmitted symbiont, Microspodka MB, was found to be present in An. arabiensis populations in Kenya, and laboratory studies indicate infection with this microsporidian limits the development of Plasmodium falciparum, suggesting it could be investigated as an additional malaria control measure (Herren et al. 2020).

The development of transgenic mosquito lines carrying both an effector molecule to prevent the development of specific pathogens inside the mosquito, and a coupled gene drive to allow this transgene to spread through populations even if the effector gene harbors a fitness cost has long been a goal in this field. With developments in Cas9 and guide RNA technology, major steps toward this goal are being taken. A gene drive strain was developed for An. gambiae which targets the cardinal gene and results in a red-eye phenotype. In small cage trials introduction of gene-drive males led to the full sexual sterilization and results in a red-eye phenotype in Cas9 and guide RNA technology, major steps toward this goal are being taken. A gene drive strain was developed for An. gambiae which targets the cardinal gene and results in a red-eye phenotype. In small cage trials introduction of gene-drive males led to the full sexual sterilization and results in a red-eye phenotype (Pollegiono et al. 2020).

Human-Mediated Environmental Influences on Vectorial Capacity and Behavior
A number of studies have been investigating the circadian or seasonal rhythms of mosquitoes and how these may be affected by human-mediated changes in environmental light intensity. Additional work on the molecular basis of circadian rhythms is likewise advancing. For instance, a study of the regulation of circadian rhythms in diurnal and nocturnal mosquito species [Ae. aegypti and Anopheles coluzzii (Coetzee & Wilkerson)] found differences in daytime light avoidance behavior, and PERIOD proteins cycled in opposite phases between two species of mosquitoes, suggesting these circadian clock protein phases may underlie differences in nocturnal and diurnal behaviors (Baik et al. 2020). Human changes to light patterns and disruptions of normal circadian rhythms due to ‘artificial light at night’ (ALAN) affect a wide range of animals. For Ae. aegypti, it appears ALAN may increase their tendency to bite humans at times when they normally would not, at least in laboratory cages (Rund et al. 2020). Simulated artificial light at night was found to considerably reduce the induction of diapause in Aedes albopictus. In urban field sites, although populations showed differences in diapause induction in early September, later on, all populations reached high levels of diapause, suggesting that the effect of artificial light may be minimized due to vegetation or other factors (Westby and Medley 2020).

Other natural occurrences, such as inland flooding, are likely to occur more frequently with climate change and with changes in land use. Effects of such events on arboviral disease risk are not well understood. In a statistical analysis of Ross River virus (RRV) cases in New South Wales, Australia, it was found that Spring and Summer flooding in certain climate zones led to an increase in the probability of a summer RRV outbreak (Tall and Gatton 2020). Effects of increasing temperatures have been studied extensively for malaria and dengue, but much less so for arboviruses transmitted in temperate settings. For WNV, a study that used trait-based models predicted peak transmission around summer temperatures of 24–25°C, which matched county-level data on West Nile disease incidence (Shocket et al. 2020). This suggested that with increasing temperatures, climate effects on transmission will be strongly location-dependent and either positive or negative. The effects of temperature on adult mosquito survival differed in interesting ways from tropical vectors that have been assessed previously, with a linear decline in survival as a function of increasing temperature (Shocket et al. 2020). In Coastal California, the use of spatio-temporal machine learning algorithms identified inhibitory, promoting, and transitional temperature bands, and found that parts of the state where summer temperatures passed the transitional zone more frequently saw the greatest expansion of West Nile positive mosquito pools over a ten-year period (Skaff et al. 2020). This could potentially help further pinpoint areas where climate change could lead to future increases in WNV transmission. Similar temperature-dependent models of vectorial capacity also may be used to understand variation in urban settings, where a mosaic of green space and impervious surface can lead to fine-scale temperature-driven variation in vector-borne disease risk. This was illustrated in Athens, GA, for Aedes albopictus, where urban areas with patches of trees led to the highest predicted vectorial capacity, a result of buffering in such areas against more extreme day- and night-time temperatures, resulting in temperatures that stay more closely to the thermal optimum of this species (Wimberley et al. 2020).

Conclusion
The field of vector-borne diseases is continually changing as a result of many of the factors that have been highlighted in this review, including range expansions or shifts of vector species, changes in land use and host distributions due to human activity and development, and climate change and other human-mediated environmental changes. These shifts offer tremendous potential as natural experiments; for instance, by perturbing transmission cycles, as evidenced by many of the papers discussed here. It also highlights the need for multidisciplinary, collaborative approaches, increased funding, and continued research on vector behavior, life history, genetics, and ecology, in order to improve our understanding of transmission...
cycles of established and emerging vector-borne diseases, the consequences of range expansions of invasive vectors, and to improve our surveillance capacity and develop sustainable, integrated vector control measures.

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