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Editorial: Factors Affecting Host Selection by Mosquitoes: Implications for the Transmission of Vector-Borne Pathogens

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Editorial on the Research Topic

Factors Affecting Host Selection by Mosquitoes: Implications for the Transmission of Vector-Borne Pathogens

Host selection by insect vectors, including mosquitoes, represents a key step in the transmission dynamics of vector-borne pathogens by affecting the ecological interactions between infected and susceptible hosts and competent vectors (Yan et al., 2021). But what are the mechanisms underlying these processes in nature? And what are the relative roles of vector-related and host-related factors in shaping host-vector interactions and how pathogens may influence these interactions? Understanding factors governing host-mosquito-pathogen interactions and their potential effects on the transmission of mosquito-borne pathogens is challenging and calls for multidisciplinary approaches. This Research Topic (RT), through seven original research articles and four reviews, addresses some key factors related with both hosts and vectors ultimately determining heterogeneities in host selection by mosquitoes, and their consequences for pathogen transmission. Here, authors explored the effects of host traits on vector attraction, such as their microbiota, the emission of different cues and how all these may be altered by host infection status. The mosquito feeding preferences, their own microbiota and the degree of specialization of pathogens in insect vectors are also addressed here, with special focus on the epidemiological consequences of these processes. In sum, the interrelated questions explored in this Research Topic greatly contribute to expanding our understanding of host-vector-pathogen interactions and importantly, of pathogen epidemiology.

Factors affecting host selection by mosquitoes.

Host selection by mosquitoes is a complex behavior that includes different phases from the location of hosts to blood feeding. Vectors use a diversity of cues to detect their bloodmeal sources (Yan et al., 2021). In this RT, authors tested the role of both chemical and auditory cues potentially affecting the interactions between bloodsucking insects and wild birds. Tomás et al. investigated the effect of bird-derived cues on mosquito attraction using traps baited with either begging calls of nestling hoopoes (*Upupa epops*) or chemical cues derived from birds (i.e., uropygial secretion of hoopoe nestlings or bacteria isolated from uropygial secretions) or nests in different habitats of southern Spain. Although they did not find support for the role of auditory cues affecting mosquito captures, mosquitoes were less abundant in traps baited with bacteria or with nest material than in traps without these stimuli. Moreover, in a blue tit (*Cyanistes caeruleus*) population breeding in

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nest-boxes in central Spain, Castaño-Vázquez et al. studied the role of carbon dioxide (CO_2) and methane (CH_4) as potential cues used by host-seeking haematophagous vectors. The abundance of *Culicoides,* the main vector of the avian malaria-like parasite *Haemoproteus*, positively correlated with the difference in CO_2 between inside and outside nest-boxes, suggesting that *Culicoides* could use this cue to locate their hosts. Altogether, results from these studies provided evidence for the role of avian derived components on vector-bird interactions with both attractive and repellent effects.

The infection status of vertebrate hosts has also been identified as a potential driver determining their susceptibility to mosquito attacks through their effects on host behavior and/or the emission of different cues. The host manipulation hypothesis (Poulin, 1998) argues that parasites are able to modify host traits to increase the chances of parasites to complete their development. Cozzarolo et al. reviewed evidence supporting this hypothesis concerning the interactions between vertebrate hosts and different groups of flying haematophagous insects. Although contradictory results arose, authors found support for enhanced attraction of vectors to infected vertebrates compared to uninfected ones in numerous vertebrate-parasite systems, with examples in, among others, birds and mammals, including humans. This was especially the case for the mosquito-borne *Plasmodium* spp. infecting birds, which were further investigated by Santiago-Alarcon and Ferreira in this RT.

Recently, a novel research area has emerged to assess the role of host microbiota affecting the interactions between vertebrates and parasites, including the contact rates between hosts and mosquitoes. Ruiz-López reviewed the role of host microbiota in mosquito behavior and shows that different host traits including sex and age, genetics, behavior, environmental conditions and, even pathogen infections may determine changes in host microbiota and, potentially, in the odor profiles of vertebrates. The uropygial gland secretion of birds and their volatile compounds are becoming the focus of studies addressing the effect of chemical cues and their interaction with pathogen infection on vector attraction. However, evidence in this regard is not conclusive, as shown in this RT, pointing toward the existence of complex relationships between different host traits, including the microbiota, in shaping their odor profiles.

After reaching their hosts, mosquito females feed on blood to obtain the resources to develop their eggs and complete their life cycle. Different approaches have been used to identify the origin of bloodmeals of mosquitoes captured in the wild (Borland and Kading, 2021). Among them, molecular tools are cost effective, sensitive and specific to accurately identify the hosts of mosquitoes with a bloodmeal in their abdomen. These studies allow researchers to identify interspecific differences in the blood feeding patterns of mosquitoes. For instance, González et al. trapped mosquitoes across an urban-to-wild habitat gradient in northern Spain and found that the species *Culex pipiens*, *Culiseta fumipennis*, and *Culiseta morsitans* fed exclusively on birds, despite the presence of mammals in the area, including humans (*Homo sapiens*) and dogs (*Canis familiaris*). In addition, Hernández-Triana et al. successfully identified the bloodmeal sources of eight species of mosquitoes of the genera *Aedes*, *Culex*, and *Psorophora* from Mexico. In this study, *Cx. quinquefasciatus* was the most frequently sampled species and showed the highest diversity of hosts, revealing its capacity to bite different species of birds such as chickens (*Gallus gallus*) or Great-tailed grackles (*Quiscalus mexicanus*) and mammals. The ability of some mosquito species to feed on different vertebrate groups was further supported by West et al. who found that *Cs. melanura* was able to feed on birds (49.3%), reptiles (34.7%), and mammals (16.0%).

What are the implications of mosquito feeding behavior for the transmission of vector-borne pathogens?

The ability of mosquitoes to feed on hosts from different groups has epidemiological consequences for the transmission of vector-borne parasites, including zoonotic pathogens. For instance, the widespread West Nile virus (WNV) is a flavivirus naturally circulating between birds and mosquitoes, but if an infected mosquito feeds on humans or horses, they can transmit the virus and potentially produce West Nile fever, despite these mammals being dead-end hosts for the virus. Furthermore, the Eastern equine encephalitis virus (EEEV) is a mosquito-borne pathogen infecting birds. As in the case of WNV, horses and humans are susceptible to EEEV infections when bitten by infected mosquitoes, but again, they are considered dead-end hosts. Thus, the contact rates between mosquitoes, susceptible vertebrate hosts and reservoirs represent basic information to be included in epidemiological studies (e.g., calculations of vector capacity). Using their data on mosquito bloodmeal sources in Florida during 2018, together with information such as mosquito abundance, parity, and temperature, West et al. provided support for the links between seasonal variation in vectorial capacity and epizootic spillover of EEEV in the area.

Furthermore, some key parameters included in the calculations of vector capacity of mosquitoes for the transmission of different mosquito-borne pathogens are also affected by mosquito-related factors. Among others, authors have recently found support for the role of mosquito microbiota in the development success of pathogens in mosquitoes and the survival cost of infections (Martínez-de la Puente et al., 2021), potentially affecting the epidemiology of vector-borne pathogens. In spite of its relevance to mosquito-pathogen interactions, there is a clear knowledge gap in the microbiota composition of wild mosquitoes from different areas and their consequences for pathogen transmission. To partially fill this gap, Tainchum et al. studied the abdominal microbiota of different species of *Anopheles* from Thailand and found 24 bacterial genera. The most abundant species captured *Anopheles minimus* presented a higher bacterial diversity than the other sampled *Anopheles* species. Unfortunately, only a single mosquito was infected by *Plasmodium* parasites, so further research on the role of *Anopheles* microbiota in the transmission capacity of mosquitoes in the area was not possible.

The feeding patterns of mosquitoes and the degree of specialization of parasites in their vectors may also have consequences for the ecology and evolution of wild host-parasite interactions. Gutiérrez-López et al. reviewed the importance of the specialization of avian *Plasmodium*, a widespread pathogen infecting birds, in mosquitoes for the transmission of this

parasite. They highlighted the need to study simultaneously the three actors involved in these interactions, i.e., hosts, mosquitoes and parasites, to better understand how host choice by mosquitoes may impact the distribution of parasites in natural settings. Different selective pressures such as those imposed by environmental factors may also contribute to the evolution of mosquito traits affecting their host seeking and blood-feeding behavior, further affecting mosquito population structure and interspecific interactions. López-Mercadal et al. investigated morphological diversity of wing patterns of the invasive Asian tiger mosquito (*Aedes albopictus*) in the Balearic Islands, Spain. These authors found strong evidence of sexual dimorphism of wing shape, which was explained on the basis of ecological and life-history factors, in particular blood-feeding behavior and oviposition.

In sum, the studies included in this RT provide valuable information, including novel research and review articles, on the factors determining the contact rates between vertebrate hosts and insect vectors, with a special focus on mosquitoes. Among others, host microbiota and the infection status by vector-borne pathogens may affect the susceptibility of vertebrate hosts to mosquito attacks by influencing the release of different cues. The biting preferences of mosquitoes to feed on blood from specific host groups or species together with mosquito-related factors such as mosquito's microbiota, may affect the development success of pathogens in mosquitoes and their epidemiology under natural conditions.

AUTHOR CONTRIBUTIONS

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