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Review

Mosquitoes feeding on ectothermic hosts: from host seeking to pathogen transmission

Joanna M Reinhold[1] and Chloé Lahondère[1,2,3,4,5]

While much research has centered on mosquitoes transmitting pathogens to mammals and birds, several species feed on cold-blooded hosts, including amphibians, reptiles, fish, and various invertebrates. Despite limited knowledge about these alternative feeding habits, delving into their biology offers valuable insights into the evolutionary origins of blood feeding and aids in developing comprehensive epidemiological models for vector-borne diseases. This review sheds light on these 'alternative' hosts, highlighting recent discoveries in this field and probing into the evolutionary theories surrounding blood feeding in mosquitoes. Additionally, we delve into the host-seeking cues used by ectotherm-feeding mosquitoes and the physiological and mechanical challenges inherent in feeding on cold-blooded animals, contrasting them with endotherm-feeding mosquitoes. Finally, we examine the pathogens these mosquitoes can transmit. While our understanding of mosquitoes with alternative hosts remains incomplete, this review synthesizes existing knowledge, offering insights into the biology and ecology of mosquito species that target cold-blooded hosts.

Addresses
[1] Department of Biochemistry, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA
[2] The Fralin Life Science Institute Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA
[3] Center of Emerging, Zoonotic and Arthropod-borne Pathogens, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA
[4] The Global Change Center, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA
[5] Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

Corresponding author: Lahondère, Chloé (lahondere@vt.edu)

Current Opinion in Insect Science 2024, **66**:101273

This review comes from a themed issue on **Special Section on Vector sensory ecology**

Edited by **Marcelo Lorenzo, Sharon Hill, Rickard Ignell** and **Claudio Lazzari**

Available online 26 September 2024

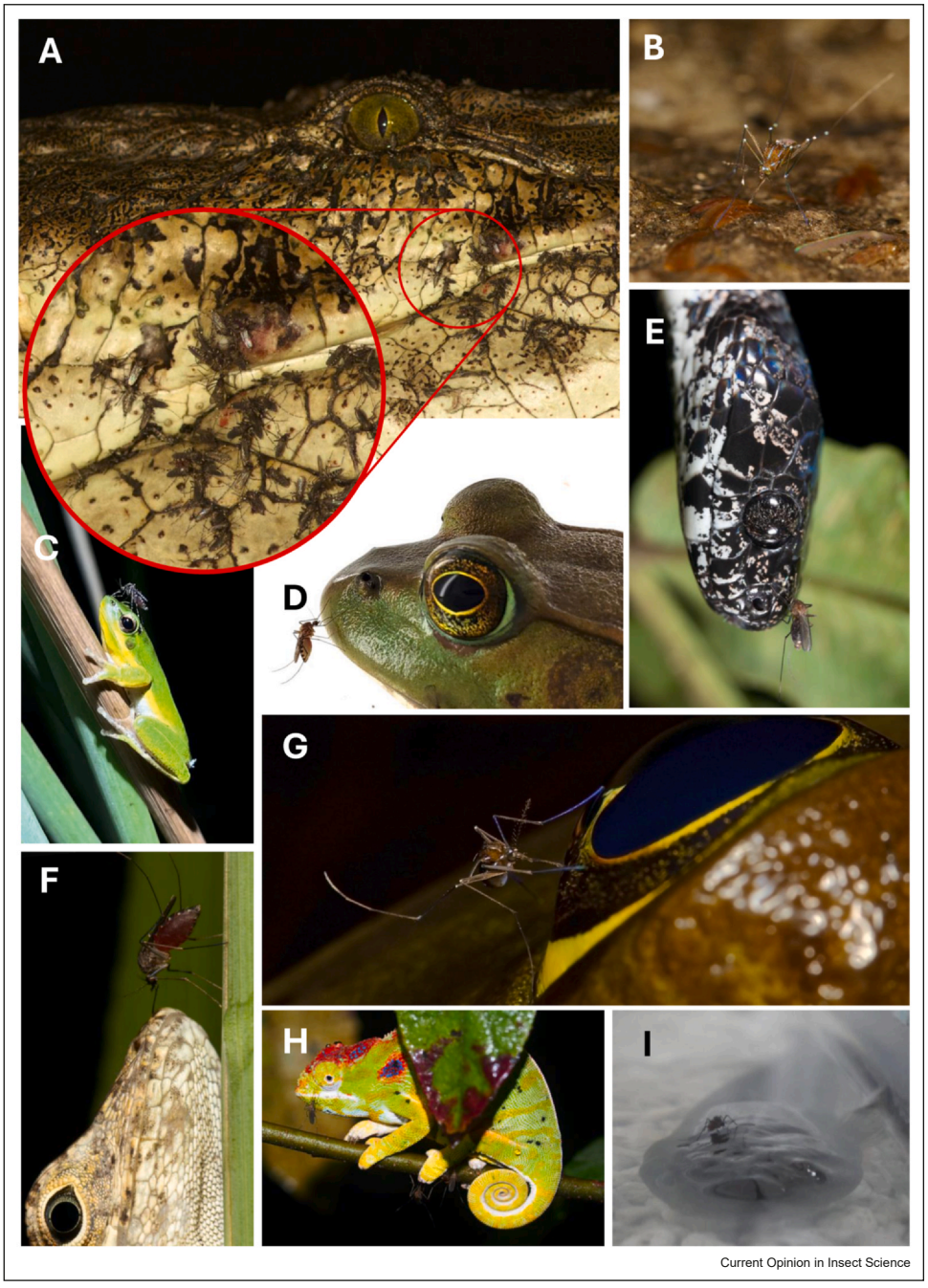
https://doi.org/10.1016/j.cois.2024.101273

Introduction

Mosquitoes, existing on this planet for over 200 million years, have evolved to become the deadliest animal globally [1–3]. With a staggering diversity of more than 3500 species across 112 genera, mosquitoes exhibit a broad spectrum of biological and ecological traits, including their host preference [2]. Mosquitoes can be either generalists, feeding on a wide array of hosts, or specialists, feeding on one particular type of host. While some species preferentially feed on endotherms, including mammals and birds, others feed on ectotherms, such as reptiles and amphibians [4–14], fish [15–18], annelids [19,20], or caterpillars [2,21] (Figures 1 and 2; Table 1). Blood contains nutrients that are primarily invested in egg development, or vitellogenesis, and it has been shown in several species, including *Aedes aegypti*, *Aedes albopictus*, *Anopheles gambiae*, *Culex quinquefasciatus*, and *Culex pipiens*, that feeding on their primary host increases their fecundity [22]. However, some species, including *Cx. pipiens* and *Cx. tarsalis*, are autogenous and can produce their first batch of eggs without a blood meal [23,24] and others such as *Toxorhynchites* spp. do not require a blood meal to complete their gonotrophic cycle [25,26]. Importantly, blood is not the primary source of nutrients for mosquitoes [27]. Similar to many other insects, females and males use carbohydrates from sources such as flowers, fruits, and tree sap for energy [28,29], and this constitutes the only food source for male mosquitoes.

Several species, including *An. gambiae*, *Ae. aegypti*, and *Cx. pipiens*, have been at the center of the research effort, mostly because of the many pathogens (e.g. *Plasmodium falciparum*, dengue virus, West Nile virus) they can transmit to humans that cause up to a million deaths each year [3]. However, the significance of mosquitoes that feed on nonhuman hosts and more specifically ectotherms, particularly in the context of the current sixth great extinction [30], underscores the need for a comprehensive understanding of the role that these species play in pathogen transmission cycles. Here, we review current knowledge on mosquito species that feed on so-called 'alternative hosts', with a particular focus on amphibians, reptiles, and invertebrates. We first discuss the evolution of blood feeding in mosquitoes as well as cues used to locate ectothermic hosts. Second, we analyze the challenges associated with feeding on cold, viscous blood. Finally, we emphasize the importance of

Figure 1



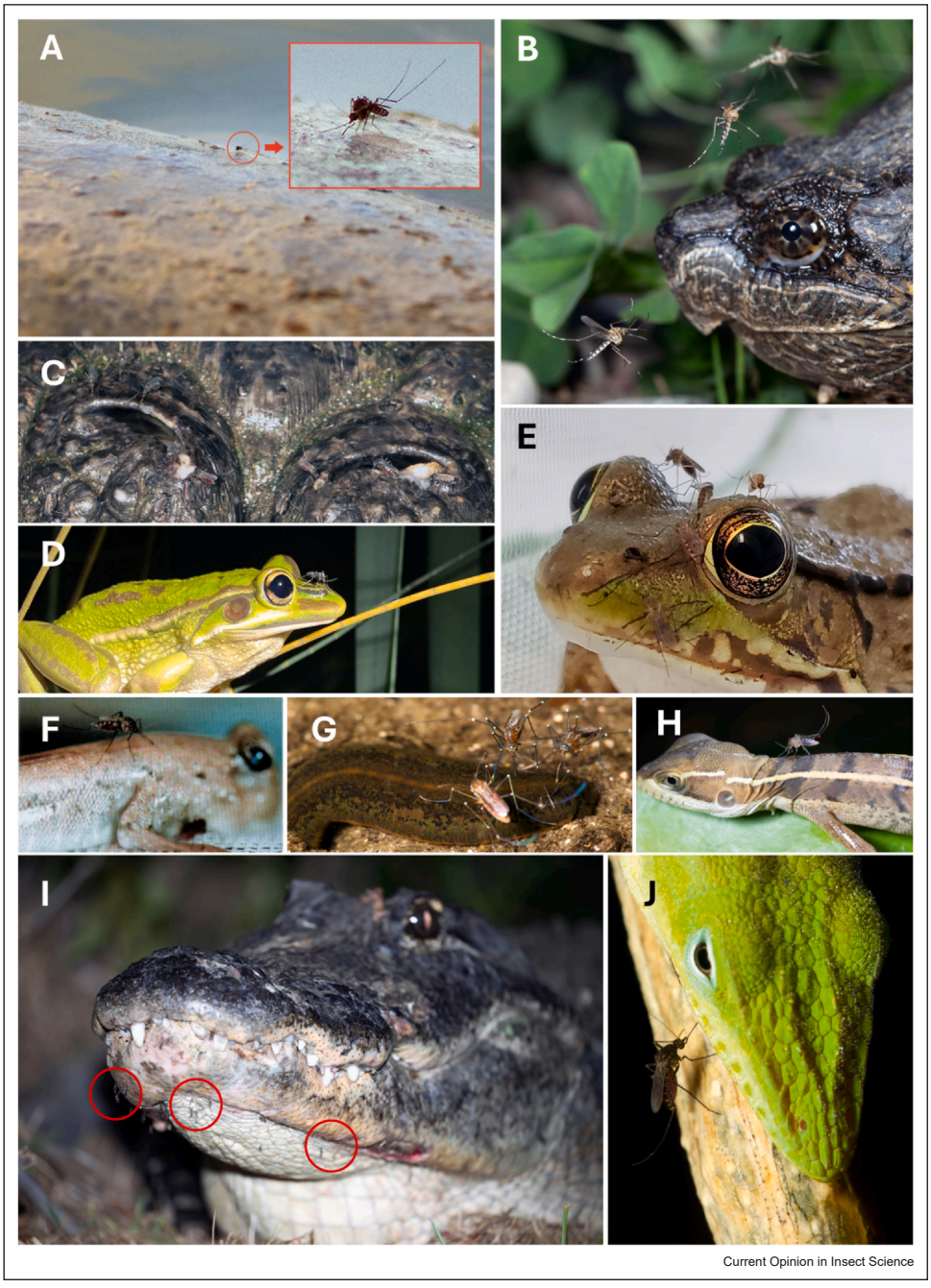
Example of ectothermic hosts targeted by mosquitoes for blood meal intake. **(a)** *Aedes taeniorhynchus* feeding on a crocodile, credit: Lawrence Reeves; **(b)** *Uranotaenia sapphirina* feeding on *Sparganophilus* sp, credit: Lawrence Reeves; **(c)** *Mimomyia elegans* feeding on the nose of *Litoria fallax*, Australia, credit: John Gould; **(d)** *Culex territans* feeding on *Rana clamitans*, credit: Joanna Reinhold; **(e)** *Culex Melanoconion* sp. feeding on *Sibon nebulatus* (Costa Rica), credit: Lawrence Reeves; **(f)** *Culex Melanoconion* sp. feeding on *Anolis sagrei*, credit: Lawrence Reeves; **(g)** *Uranotaenia lowii* feeding on the eyeball of *Rana catesbeiana*, credit: Lawrence Reeves; **(h)** *Culex* spp. mosquitoes feeding on the mouth and foot of an adult female *Furcifer minor* (Lesser Chamelon; Madagascar). Small black spots on the body indicate prior mosquito bite sites, credit: Devin A. Edmonds; **(i)** *Aedes baisasi* feeding on *Bostrychus sinensis*, credit: Takashi Miyake.

mosquitoes that feed on animals other than humans in getting insight into the biology of human disease vectors and into pathogen transmission in ectothermic hosts.

Evolution of blood feeding and host-seeking

Because not all mosquito species require a blood meal to develop eggs, the question arises as to how and why

Figure 2



Example of ectothermic hosts targeted by mosquitoes for blood meal intake. **(a)** *Culex Melanoconion* sp feeding from a manatee (Florida Everglades USA), credit: Lawrence Reeves; **(b)** *Aedes canadensis* swarming *Chelydra serpentina* (Minnesota, USA), credit: Lawrence Reeves; **(c)** *Culex Melanoconion* biting the nose of *Alligator mississippiensis*, credit: Lawrence Reeves; **(d)** *Mimomyia elegans* feeding on the nose of *Litoria aurea* (Australia), credit: John Gould; **(e)** *Culex territans* feeding on *Rana clamitans*, credit: Joanna Reinhold; **(f)** *Aedes baisasi* feeding on a mudskipper, credit: Haruo Okudo; **(g)** *Uranotaenia sapphirina* feeding on a leech, credit: Lawrence Reeves; **(h)** *Culex nigripalpus* on a lounging *Basiliscus basiliscus* (Costa Rica), credit: Lawrence Reeves; **(i)** *Anopheles crucians* feeding on *Alligator mississippiensis*, credit: Dr. Lawrence Reeves; **(j)** *Culex (Melanoconion)* sp. feeding on *Anolis carolinensis*, credit: Lawrence Reeves.

blood feeding has emerged among these insects and whether it constitutes the ancestral trait. Several studies suggest that mosquitoes were originally phytophagous because all species require carbohydrates to survive and possess the digestive enzymes to process plant matter [29,31]. Blood feeding may have also evolved due to

Table 1

Pathogens transmitted to ectothermic hosts by mosquitoes. '*' denotes transmission under laboratory conditions only.

Mosquito species	Preferred host (s)	Alternative host (s)	Geographic distribution	Pathogens transmitted	References
Aedes aegypti	Mammals (humans)	Reptiles	Tropical (global)	Yellow fever virus, Dengue virus, Zika virus Chikungunya virus, *Hepatozoon* sp.*, *Plasmodium* sp., *Oswaldofilaria belemensis**, *Foleyella* sp.*	[66,77,78]
Aedes africanus	Mammals	Reptiles (lizards)	Africa (sylvatic)	Yellow fever virus, Zika virus; *Plasmodium giganteum*	[66,79]
*Aedes albopictus**	Mammals	Reptiles*, amphibians*	tropical/subtropical (global)	Yellow fever virus, Dengue virus, Zika virus Chikungunya virus, *Dirofilaria immitis, Plasmodium* sp. (avian)	[66,79]
Aedes apicoargenteus	Mammals (humans)	Reptiles (lizards)	Africa	Chikungunya virus, Zika virus, *Plasmodium giganteum*	[66,79]
Aedes atlanticus	Mammals (humans)	Reptiles	Southeastern US	Yellow fever virus, Keystone virus	[6,80,81]
Aedes baisasi	Fish		Asia	No data	[16–18]
Aedes canadensis	Reptiles, mammals	Bird	Temperate	La Crosse virus, *Dirofiliaria immitis*	[6,81]
Aedes longiforceps	Mammals (humans)	Fish (mudskipper)	Asia	No data	[82]
Aedes sierrensisa	Mammals	Snake	Western USA	*Dirofiliaria immitis, Hepatozoon rarefaciens**	[66,83]
Aedes simpsoni	Mammals	Reptiles (lizards)	Africa	Yellow fever virus, *Plasmodium giganteum*	[66,77,84]
Aedes taeniorhynchus	Reptiles (crocodile)	Manatee	Southeastern US	Eastern equine encephalitis virus, Venezualan equine encephalitis virus, *Dirofilaria immitis*	[85,86]
*Aedes togoi**	Mammals, birds	reptiles*, amphibians*	Asia, North America	Japanese encephalitis virus, *Brugia malayi*, *Dirofilaria immitis*, *Wuchereria bancrofti*	[15,87]
Aedes triseriatus	Mammals, birds	Reptiles (turtles)	North America	La Crosse virus, West Nile virus	[81]
Aedes vexans	Mammals, birds	Reptiles (alligator), amphibians*	Tropical/subtropical (global)	Zika virus	[15,64]
*Anopheles albimanus**	Mammals (humans)	Snake	Central and South America	Mayaro virus, O'nyong-nyong, Sindbis virus, *Hepatozoon rarefaciens**, *Plasmodium falciparum*, *Plasmodium vivax*	[66,88]
Anopheles atropos	Mammals (humans)	Manatee	Southeastern US, Central America	*Plasmodium vivax*	[86,89]
Anopheles stephensi	Mammals	Caterpillars, reptiles	Africa and Asia	*Hepatozoon domerguei**, *Oswaldofilaria bascillaris*, *Foleyella* sp.*, *Plasmodium falciparum*, *Plasmodium vivax*, *Saurositus agamae hamoni**	[21,66]
Anopheles vagus	Mammals, birds	Mudfish*	India, Asia	Japanese encephalitis virus, *Plasmodium falciparum, Plasmodium vivax, Wuchereria bancrofti*	[90]
*Armigeres subalbaius**	Mammals, birds	Reptiles*, amphibians*	Asia	*Brugia pahangi*, *Wuchereria bancrofti*	[15]
Culex annulirostris	mammals, birds	Reptiles (lizards)*	Australia, Pacific Islands	Barhma Forest virus, Kunjin virus, Murray valley encephalitic virus, Ross River virus, West Nile virus, *Dirofilaria immitis*, *Oswaldofilaria chlamydosauri**, *Wuchereria bancrofti*	[66,91]
Culex (Micraedes) antillummagnorum	Reptiles (anoles)	-	Southeastern United States	*Plasmodium* spp.	Reeves et al., personal communication
Culex (Melanoconion) atratus	Reptiles	Mammals	Southeastern United States	No data	[9]

Table 1 (*continued*)

Mosquito species	Preferred host (s)	Alternative host (s)	Geographic distribution	Pathogens transmitted	References
Culex erraticus	Birds, mammals	Reptiles	North America	Eastern equine encephalitis virus, Venezuelan equine encephalitis virus, St. Louis encephalic virus, West Nile virus, *Plasmodium floridense*	[66,92,93]
Culex fuscanus	Mudfish*	-	Asia	No data	[90]
Culex h. ryukyuans	Amphibians (frogs)	-	Japan	No data	[18]
Culex hayashii	Amphibians (frogs)	-	Japan	No data	[15,94]
Culex infantalus	Small mammals, birds, amphibians, reptiles	-	Asia	No data	[15,18,94]
Culex (Melanoconion) iolambdis	Birds, reptiles, amphibians	Sea mammals (manatee)	Southeastern United States, tropical Americas	Venezuelan equine encephalitic virus	[86,95]
Culex lineata	Lizards	-	Africa	*Hepatozoon affluomaloti*	[66]
Culex nigrepalpus	Birds, mammals	Reptiles, amphibians	Southeastern United States, Central America	St. Louis encephalitic virus, West Nile Virus	[96,97]
Culex peccator	Amphibians, reptiles	-	Southeastern United States, Central America	*Amblyospora* sp.*	[61,81]
Culex (Melanoconion) pilosus	Reptiles	Birds, mammals	Southeastern United States	No data	[9]
*Culex pipiens (pallens; molestus)**	Mammals, birds	Reptiles*, amphibians*	Temperate and subtropical regions worldwide	West Nile Virus, Japanese encephalitis virus, Usutu virus, Rift Valley fever virus, Sindbis virus, Tahyna virus, *Dirofilaria immitis*; *Plasmodium* sp. (avian), *Hepatozoon* sp.*, *Saurocytozoon tupinambi, Garnia morulum, Oswaldofilaria* sp.*, *Foleyellides* sp.*	[15,66,96]
Culex quinquefasciatus	Birds, mammals	Reptiles	Tropical and subtropical regions worldwide	St. Louis encephalitis virus, West Nile Virus, Western equine encephalitis virus, *Wuchereria bancrofti, Plasmodium* sp. (avian), *Schellackia landaue, Hepatozoon* sp.*, *Conispiculum flavescens**, *Oswaldofilaria* sp.*, *Foleyellides* sp.*, *Macdonaldius innisfailensis**, *Bd**	[66,81,96]
Culex tarsalis	Birds, mammals	Reptiles	Southeastern United States, Central America	St. Louis encephalitis virus, Western equine encephalitis virus, West Nile virus, *Hepatozoon fusifex*	[66,96]
Culex territans	Amphibians, reptiles	Birds, mammals	Temperate/subtropical in Northern Hemisphere	Ranaviruses, *Hepatozoon* sp.*, *Plasmodium floridense, Trypanosoma* sp., *Foleyellides flexicauda*; *Bd**	[4,5,7,11,66,81]
*Culex tritaeniorhynchus summorosus**	Mammals (humans, large cattle), birds	Reptiles*, amphibians*	Asia, Northern Africa	Japanese encephalitis virus	[15]
Culiseta melanura	Birds	Reptiles	North & Central America	Eastern equine encephalitis virus	[81]
Deinocerites cancer	Birds, mammals	Reptiles, amphibians	Southern Florida (USA), Central America, Bahamas, Cuba, Greater Antilles	No data	[98]
Deinocerites dyari	Reptiles	Birds, mammals	Central & South America	No data	[98]
Deinocerites epitedeus	Reptiles	Birds, mammals, amphibians	Texas (USA), Central America	No data	[98]
Deinocerites pseudes	Mammals, birds, reptiles	Amphibians	Central & South America	Venezuelan equine encephalitic virus	[98,99]

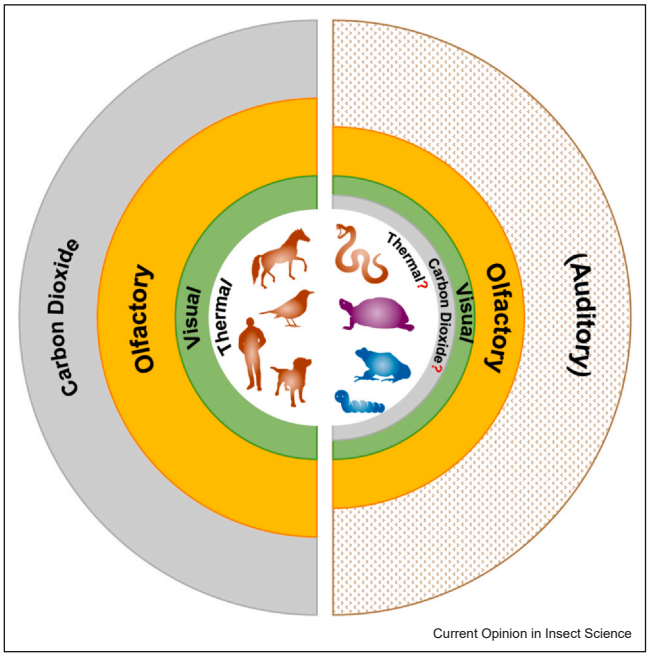
Table 1 (*continued*)

Mosquito species	Preferred host (s)	Alternative host (s)	Geographic distribution	Pathogens transmitted	References
Mansonia dyari	Mammals, birds	Reptiles (alligators)	Southeastern United States, Central America	Venezuelan equine encephalitic virus, Rift Valley fever virus, *Dirofilaria immitis*	[93,100]
Mansonia titillans	Mammals, birds	Reptiles	Southeastern United States, Central & South America	Venezuelan equine encephalitic virus, Rift Valley fever virus, *Dirofilaria immitis*	[93,100]
Mansonia uniformis	Mammals, birds	Mudfish	Africa, Asia, Australia	*Brugia malayi, Wuchereria bancrofti*	[90,101]
Mimomyia chamberlaini	Amphibians (frogs)	-	Asia, Australia	No data	[102]
Mimomyia elegans	Amphibians		Asia, Australia	No data	[18,57]
Mimomyia luzonensis	Amphibians (toads)	-	Asia, Australia	No data	[103]
Mimomyia mediolineata	Amphibians		Asia, Australia	No data	Reeves (personal communication)
Psorophora ferox	Mammals, birds	Reptiles*	Southeastern US	Rocio virus, Venezuelan equine encephalitis virus, West Nile virus, *Dermatobia hominis* larvae	[90,104]
*Tripteroides bambusa**	Mammals, birds	Reptiles*	Asia, North America	*Plasmodium* sp. (avian)	[15,105]
Uranotaenia annandalei	Amphibians		Asia	No data	[12]
Uranotaenia argyrotarsis	Amphibians (frogs)		Asia, Australia	No data	[58]
Uranotaenia bimaculata	Amphibians (frogs)	-	Asia	No data	[15]
Uranotaenia jacksoni	Amphibians	Reptiles	Asia	No data	[12,18]
Uranotaenia lateralis	Mudskippers		Asia	No data	[14,18]
Uranotaenia lowii	Amphibians		North, Central & South America	No data	[57]
Uranotaenia macfarlanei	Amphibians (frog, newt)		Asia	No data	[14,18]
Uranotaenia mashonaensis	Amphibians		Africa	Nounané virus, *Dactylosoma kermiti, Neofileyellides boerewors*	[67,68,106]
Uranotaenia montana	Amphibians		North, Central & South America, Africa	*Neofileyellides boerewors*	[68]
Uranotaenia nivipleura	Amphibians		Asia	No data	[14,18]
Uranotaenia novobscura ryukyuana	Amphibians		Asia	No data	[107]
Uranotaenia ohamai	Amphibians	Fish (mudskipper)	Asia	No data	[14,18]
Uranotaenia sapphirina	Amphibians	Annelids	North America	Eastern equine encephalitis virus, West Nile Virus	[20]
Uranotaenia unguiculata	Amphibians		Europe, Northern Africa, Middle East, Asia	West Nile virus, *Dirofilaria repens*	[40]
Uranotaenia yaeyamana	Amphibians		Asia	No data	[14,18]

feeding on protein-rich sweet substances, such as insect honeydew, creating a path from phytophagy to entomophagy, and ultimately hematophagy. Access to food rich in proteins such as pollen could have also contributed to the specialization of the proboscis to pierce tissues and of metabolic pathways to process and utilize protein [28,29]. However, Soghigian et al. [2] present blood feeding as an ancestral trait, with amphibians likely being the initial hosts before mosquitoes diversified their feeding habits across reptiles, birds, and mammals. Interestingly, the closest mosquito relatives, *Corethrellidae*, also feed on amphibians, implying the common ancestor may have been an amphibian feeder as well [32]. Finally, males seem to also have exhibited hematophagy in the past, as recent fossil records of *Libanoculex* indicate that their mouthparts presented characteristic features associated with blood feeding, including sharp and denticulate mandibles [1].

Mosquitoes use a variety of long- and short-range sensory cues when host-seeking and synchronize with their preferred host either spatially, temporally, or both. For example, *Culex territans* exhibit similar diapause, daily activity pattern, and location to one of their primary hosts, *Rana clamitans* [33,34]. Similarly, certain reptile-feeding mosquitoes such as *Culex erraticus*, overwinter in gopher tortoise burrows, thus providing rapid access to a blood meal when exiting diapause [8]. While much attention has been directed toward mosquitoes feeding on endotherm hosts, the cues utilized for locating ectothermic hosts remain poorly understood. To find a warm-blooded host, mosquitoes follow plumes of carbon dioxide (CO_2), body odors, as well as thermal and visual cues [35,36] (Figure 3). However, ectothermic hosts typically lack a thermal signature, unless actively basking in the case of reptiles. Furthermore, amphibians and certain invertebrates such as annelids breathe cutaneously, resulting in a more diffused CO_2 plume compared with endothermic hosts [37,38]. Other studies have revealed that *Cx. territans*, *Uranotaenia unguiculata* and *Uranotaenia lowii*, respond to auditory cues such as male frog mating calls [39–41] (Figure 3). However, *Cx. territans* are also attracted and will readily feed on female and noncalling frogs, which supports the evidence that this species relies on other cues, including visual and olfactory, to locate these hosts [34]. Differences in sensilla have been suggested to influence the mosquitoes' ability to detect different odor profiles. Specialists, such as *Cx. territans*, possess fewer sensilla or fewer types compared with generalists such as *Cx. pipiens* and *Ae. aegypti* [42]. Interestingly, this species possesses the types of sensilla required for heat and CO_2 sensing (i.e. coeloconica at the tips of the antennae, bulb organs on the palps, respectively) and in larger numbers than *Toxorhynchites* spp. [42,43]. However, a recent behavioral study showed a lack of attraction to thermal and CO_2 cues presented either separately or simultaneously [44],

Figure 3



Long- and short-range host-seeking cues used by mosquitoes to locate and feed on endotherms (left panel) and ectotherms (right panel). (Left panel) Carbon dioxide serves as a long-range cue for most endotherms, followed by olfactory (body odors) and visual cues, at a closer distance. Finally, mosquitoes use the thermal signature emanating from their hosts as a short-range cue. Once landed on the host, taste (not indicated here) also plays a role in determining the quality of the blood of the host once initiating biting. (Right panel) Mosquitoes feeding on ectotherms may use auditory cues if the hosts are able to emit calls (e.g. frogs), followed by olfactory and visual cues. Small ectotherms, in particular amphibians, do not produce a large amount of carbon dioxide, and it is unclear whether it might be used as a host-seeking cue. In the case of larger ectotherms (e.g. crocodile), which produce more carbon dioxide, it is possible that mosquitoes follow the plume to target their host. As amphibians and invertebrates are nonbasking hosts, they do not produce a heat signal. However, it is possible that reptiles such as snakes, turtles, or crocodiles, by basking, may emit a thermal signature that mosquitoes use to target them for blood-feeding.

indicating that the excitation of the neurons within the extant sensilla may elicit different behavioral responses than that on endotherm-feeding mosquitoes, such as an adverse or indifferent reaction.

Physiological and biomechanical challenges associated with feeding on ectotherms

During feeding, the cibarial and pharyngeal pumps located inside the mosquito's head contract and expand to draw blood through the proboscis. Mosquitoes that feed on warm blood benefit from the ability to feed quickly, reducing the risk of predation by minimizing their time spent on the host. However, this rapid intake of warm blood may lead to heat stress [45,46]. Nonetheless, several species have evolved mechanisms to counteract

this stress either through thermoregulation or thermotolerance [47,48]. Feeding on ectothermic hosts is associated with different challenges. Although mosquitoes most likely do not often face the threat of heat shock when feeding on ectotherms (unless hypothetically when feeding on a basking reptile), they encounter other challenges related to the ingestion of cold, viscous blood. Indeed, blood temperature affects its viscosity, influencing the time required for blood-sucking insects to feed to repletion [49,50]. Since amphibians and annelids do not bask, mosquitoes feed on their blood at ambient temperature, which is lower than the temperature of the blood of most endotherms, such as birds and mammals. Additionally, some animals, particularly amphibians, have large and oblong red blood cells, increasing the likelihood for clumping or clotting during ingestion [51]. This may explain why *Cx. territans* takes 25 min to 3 hours to feed to repletion on frogs at approximately 20°C [34,52]. Interestingly, *Aedes vexans* can exhibit a 'burst mode' pumping while feeding to potentially clear blockages and increase blood intake [53], but whether this mechanism also exists in ectotherm-feeding mosquitoes remains to be tested.

These factors can leave mosquitoes more susceptible to predation when feeding on ectothermic hosts. To mitigate predation risks, mosquitoes employ various strategies such as anesthetic in their saliva, which may be the cause of color changes in the skin of chameleons [54] (Figure 1h), as well as by selecting specialized biting sites, such as ankles (humans) or the back (frogs) [7,55] (this report; Figure 2e). *Culex territans* and *Mimomyia elegans* have been observed approaching frogs from behind, while *Uranotaenia lowii* approaches frogs by walking up to them. After landing, all three species move from the rear toward the head of the frog, but *Cx. territans* and *Ur. lowii* may feed with minimal contact with the frog, resting their bodies on the ground or nearby vegetation [7,56,57] (Reinhold and Lahondère, personal observation). *Mimomyia elegans* targets the nostril of frogs, positioning itself in the blind spot between the frog's eyes [56] (Figure 1c, Figure 2d). Similarly, *Mimomyia mediolineata* feeds from the nostrils of frogs, and *Uranotaenia argyrotarsis* has been observed feeding on the upper eyelids [58] (Reeves, personal communication). This positioning may offer advantages due to the thinner skin of the frog's nostrils or eyelids from which the mosquitoes feed in addition to being out of the frog's line of sight.

Pathogens transmitted by mosquitoes to ectotherm hosts

While mosquitoes are predominantly known for transmitting viruses and parasites to humans (e.g. yellow fever virus, dengue virus, *Plasmodium falciparum*) and other mammals (e.g. heartworm to dogs, eastern equine encephalitis virus [EEEV] to horses) and birds (e.g. West Nile virus [WNV], EEEV), their role as vectors of pathogens to ectothermic hosts has gained attention [3]. Reptiles and amphibians serve as important reservoir hosts for various zoonotic vector-borne viruses, including WNV, EEEV, western equine encephalitis, and chikungunya [10,59–64]. As reservoir hosts allow for pathogens to circulate between anthropic outbreaks, it is critical to identify the bridge vectors allowing the viruses to enter these cold-blooded hosts and re-enter the human populations (Table 1).

The first reptilian vector-borne disease is thought to occur in the Cretaceous period (found in a sandfly) [65], and mosquitoes have been shown to be competent vectors for several parasites to many ectothermic hosts since then (Table 1) [66]. Members of the *Uranotaenia* genus (*Ur. mashonaensis* and *Ur. montana*) can be vectors of several parasites to toads, including *Dactylosomoa kermiti* and *Neofoleyellides boerewors* [67,68]. Recent discoveries include the confirmation of *Cx. territans* as a vector of Giant anuran trypanosomes to amphibian hosts (Reinhold and Lahondère, unpublished data) as well as *Cx. amtillummagnorum* as a vector of reptilian malaria to anoles (Reeves, personal communication). While vector-borne parasites have been relatively well studied in amphibians and reptiles, the roles that vectors play in other pathogen transmission cycles, such as viruses, fungi, or bacteria, are relatively understudied. For example, Ranaviruses, which infect amphibians, reptiles, and fish, have been suspected to be vectored by *Cx. territans*. Kimble et al. [69] found that this species can uptake Ranaviruses under laboratory conditions, and strong evidence for transmission in the field has been shown as well (Reinhold and Lahondère, unpublished data). However, many other viruses affect herpetofauna and other alternative hosts [70], though little research has been done to investigate the role of vectors, including mosquitoes, in their transmission.

Another group of pathogens that affects amphibians and reptiles is fungi. *Batrachochytrium dendrobatidis* (*Bd*), a deadly topical pathogenic fungus, has been shown to be mechanically transmitted through contact during feeding by two *Culex* mosquitoes (*Cx. territans* and *Cx. quinquefasciatus*) [11,71], but several other pathogenic fungi may affect herpetofauna [72]. Given mosquitoes' proclivity for fungi, it is likely that they could serve as mechanical vectors of other topical fungi as well [73,74]. Additionally, existing infections with Ranaviruses have been seen to increase *Bd* infection risks [75,76]. Vector-borne bacterial diseases can also affect herpetofauna, though the majority of the known bacteria are transmitted by ticks and mites [62], and the potential role of mosquitoes has yet to be tested.

Conclusion and knowledge gaps

Expanding our knowledge on ectotherm-feeding mosquitoes offers an invaluable opportunity to decipher the evolutionary origin of blood feeding among this taxon and the role they play in pathogen transmission. While research predominantly focused on *Cx. territans* mosquitoes, a comprehensive understanding of other species is crucial. Identifying the sensory cues utilized for host-seeking and elucidating their role as vectors in disease transmission cycles are essential steps toward addressing knowledge gaps. Moreover, further research is warranted to explore the implications of these species in pathogen transmission in the context of both global amphibian population decline and human health.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Marcelo Lorenzo and Claudio Lazzari for the invitation to contribute the present review. We are grateful to Lawrence Reeves, Takashi Miyake, John Gould, Ryan Carney, Len de Beer, Devin A. Edmonds, and Haruo Okudo for providing some of the pictures highlighted in the present review. We thank Lawrence Reeves and Clément Vinauger for helpful discussion and suggestions. This work was supported in part by the NSF-IOS (Award #2114127), the Department of Biochemistry, CeZAP, and the Fralin Life Science Institute at Virginia Tech.

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