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REVIEW
OTHER

The complexities of blood-feeding patterns in mosquitoes and sandflies and the burden of disease: A minireview

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Abstract

Mosquitoes and sandflies exhibit a wide range of blood feeding patterns, targeting a wide range of vertebrate species, including birds, mammals, reptiles, and amphibians, for proteins vital for egg development. This broad host range increases the opportunity for them to acquire pathogens of numerous debilitating-and-fatal diseases from various animal reservoirs, playing a significant role in disease crossover between animals and humans, also known as zoonotic transmission. This review focuses on the intricate blood-feeding habits of these dipteran vectors, their sensory systems and the complex dance between host and pathogen during disease transmission. We delve into the influence of blood sources on pathogen spread by examining the insect immune response and its intricate interplay with pathogens. The remarkable sense of smell guiding them towards food sources and hosts is explored, highlighting the interplay of multiple sensory cues in their navigation. Finally, we examine the challenges in mosquito control strategies and explore innovations in this field, emphasizing the need for sustainable solutions to combat this global health threat. By understanding the biology and behaviour of these insects, we can develop more effective strategies to protect ourselves and mitigate the burden of vector-borne diseases.

KEYWORDS
blood feeding, diptera, hematophagy, mosquitoes, sandfly, vector

1 | INTRODUCTION

A diverse array of arthropods, including mosquitoes, sandflies, bed bugs, midges and lice, serve as vectors for a multitude of infectious organisms through hematophagy (blood-feeding). These pathogens collectively pose a substantial global health crisis, causing over 700,000 deaths annually, accounting for more than 17% of all infectious diseases (World Health Organization, 2024). Mosquitoes (Dip., Culicidae) and phlebotomine sandflies (Dip., Phlebotominae) pose a significant threat to public and veterinary health by transmitting a variety of protozoa and viral pathogens (Ready, 2013; Nouzova et al., 2019; Becker et al., 2020). The burden of the infectious diseases they transmit is substantial with incidence soaring across the globe over the years. This has been attributed, in part, to a confluence of globally acting factors, including habitat alteration, the introduction of invasive species and climatic shifts. Notably, these environmental perturbations can directly influence the prevalence of vector-borne pathogens responsible for human illnesses (Baker et al., 2022; Hui, 2006; Cuthbert et al., 2023).

Malaria alone, transmitted by *Anopheles* mosquitoes, infects 200 million individuals annually, claiming 0.6–1.2 million lives, primarily children in underprivileged nations in Africa (Bhuvaneswari et al., 2023). *Aedes* mosquitoes, known for yellow fever in the 18th and 19th centuries, currently transmit the increasingly prevalent dengue fever

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in tropical and subtropical regions (Bhatt et al., 2015; Johnson et al., 2018; World Health Organization, 2023). Dengue is a major public health issue, as over 10 million cases and at least 6500 deaths have been reported from 176 countries in 2024, with most cases affecting children aged 15 and under (The Lancet, 2024). Majority of the cases have been in Central and South America; PAHO reported a record-breaking 9 million cases by May 2024 (Pan American Health Organization/World Health Organization, 2024). The estimated annual figures for yellow fever virus are 200,000 infections and 30,000 fatal cases (Centers for Disease Control and Prevention, 2023a, 2023b). Additionally, mosquitoes spread filarial elephantiasis, West Nile virus, Rift Valley fever, Ross River fever, and encephalitis viruses (Socha et al., 2022). It is known that *Aedes* and *Aedes*-related diseases cause a cumulative economic damage of approximately US $300 billion worldwide (Roiz et al., 2024).

Sandflies transmit a diverse array of protozoan, bacterial and viral pathogens (Killick-Kendrick, 1990; Maroli et al., 2013; Tsirigotakis et al., 2018). Notably, *Leishmania* spp., single-celled flagellate protozoa with an obligate intracellular lifecycle, are transmitted between humans as well as wild and domestic animals, such as dogs and cats. Leishmania infection manifests in various forms, including cutaneous (CL), visceral (VL), mucocutaneous and diffuse cutaneous leishmaniasis. The global burden of leishmaniasis is significant, with estimations ranging from 50,000 to 400,000 cases of VL and roughly 1 million cases of CL reported annually (Alten et al., 2016; Bourdeau et al., 2020; Cecílio et al., 2022; Maroli et al., 2013). Geographically, the distribution of these cases is uneven, with nearly 90% of VL concentrated in India, Brazil, Bangladesh, Ethiopia and Sudan. Similarly, CL cases are predominantly found in Afghanistan, Ethiopia, Iran, Syria and Türkiye (Montaner-Angoiti & Llobat, 2023). Furthermore, phlebotomine sandflies can transmit a diverse array of phleboviruses, numbering approximately 60. Sandfly fever Naples virus, sandfly fever Sicilian virus and Toscana virus are prominent examples (Alkan et al., 2016). These viruses can infect humans, canines and livestock, causing a spectrum of clinical manifestations. Common symptoms include fever, nausea, vomiting and neurological complications arising from central nervous system involvement. Additionally, leukopenia (decreased white blood cell count) and thrombocytopenia (decreased platelet count) may be observed (Ergünay et al., 2020).

These vector-borne threats are unfortunately spreading and emerging in previously unaffected regions but also reemerging in areas where they were once eradicated (Franklinos et al., 2019; Jobe et al., 2024). Several factors, such as climate change, urbanization and global travel, have contributed to the spread of certain mosquito species, such as *Aedes aegypti*, *Anopheles stephensi* and *Aedes albopictus*, beyond their native habitats, potentially facilitating disease transmission and even introducing new disease risks (Cuthbert et al., 2023; Pecor et al., 2023). Consequently, dengue cases have skyrocketed globally over the past five decades, spreading to numerous new countries. Similarly, yellow fever is making a comeback in several endemic regions after significant declines. These diseases, characterized by high morbidity and mortality, pose substantial economic and societal burdens, potentially hindering economic development and impacting social and political structures (Franklinos et al., 2019). Unlike mosquitoes, sandflies exhibit limited dispersal capabilities due to their weak flight and short lifespan, precluding their establishment as invasive species. However, their geographical range can expand to adjacent territories when environmental alterations create favourable conditions for survival and reproduction. This potential for range expansion due to climate change raises concerns about their ecological impact (Koch et al., 2017; Medlock et al., 2014).

These renowned vectors of disease and nuisance biters occupy a unique position in scientific inquiry due to their impact on public health (Table 1). Driven by fundamental needs like survival and reproduction, their intricate behavioural patterns stem from highly adapted sensory systems tailored to their specific ecological niches. This interplay between life cycle, anatomy, physiology and behaviour makes them both a ubiquitous presence in human societies and a captivating subject of study. Understanding their biology, particularly their feeding behaviour, sensory perception and complex interactions with pathogens within their bodies, is crucial for developing targeted and sustainable control strategies to protect ourselves from these ever-present threats (Juma, 2024). For this review, we focused on studies investigating various aspects of blood-feeding in mosquitoes and sandflies. These aspects included: blood feeding patterns, evolutionary origins of blood-feeding (when and why blood-feeding behaviour emerged in these groups), the biological benefits gained from feeding on blood and the impact of blood meal source on development and reproduction. Studies were selected from peer-reviewed scientific journals, with a focus on field-based or laboratory experiments.

2 | MOSQUITO AND SANDFLY BLOOD FEEDING: WHY DO THESE INSECTS NEED BLOOD?

Hematophagy, the act of feeding on and metabolizing blood, is a successful feeding strategy for various animals, particularly arthropods. Blood is comprised of abundant proteins and lipids, easily accessible through piercing or sucking mechanisms, this makes it a highly nutritious and convenient food source (Krenn & Aspöck, 2012; Robert & Debboun, 2020). Anautogenous females require blood meals for vitellogenin biosynthesis, a precursor protein critical for egg development. Within the ovaries, immature eggs reside in primary chambers. Each chamber contains an oocyte (future egg cell), supportive nurse cells and enveloping follicle cells (Hansen et al., 2014; Valzania et al., 2019). Importantly, development of these chambers is arrested until a blood meal is acquired. These hematophagous arthropods ingest massive quantities of blood, often exceeding their own body weight. This necessitates rapid processing of the ingested blood to extract nutrients and eliminate excess water, enabling them to regain mobility. Blood feeding triggers a cascade of physiological responses beyond just digestion like oogenesis (egg production), immune system response and even the regeneration of midgut epithelial cells (Reynolds et al., 2020; Taracena et al., 2018).

In mosquitoes, blood ingestion initiates the vitellogenic phase of oogenesis through the release of ovary ecdysteroidogenic hormone

TABLE 1 The primary factors that influence host seeking behaviour in mosquitoes and sandflies.

Cues	Reported effect	Reference
Chemical	Chemicals released by host as a byproduct of perspiration, excretion and respiration play a vital role in mosquito and sandfly host seeking. Examples include lactic acid, ammonia, urea, uric acid, pentadecanoic, carbon dioxide, 1-octen-3-ol, undecanal, octenol, heptanoic, phenylacetaldehyde, 6-methylhept-5-en-2-one, pentadecane, icosane etc. Mosquitoes and sandflies have highly sensitive receptors that can detect short- and long-range attractants. These chemicals, often working in combination rather than isolation, include volatile organic compounds (VOCs) emitted from animals (including human foot odour), animal sheds or materials associated with such habitats (like animal dung and oviposition sites) and plants. VOCs such as 6-methyl-5-hepten-2-one, α-pinene, benzyl alcohol, m-cresol, p-cresol and decanal might be more attractive to a wider range of sandflies and mosquitoes for breeding, resting or finding blood meals	Costantini et al., 1998; Takken and Knols (1999), Dougherty et al. (1999), Rebollar-Tellez et al. (1999), Andrade et al. (2008), Bohbot and Dickens (2009), Machado et al. (2015), Tavares et al. (2018), Tavares et al. (2018), Retkute et al. (2021), Hassaballa et al. (2021), De Obaldia et al. (2022) and Bezerra-Santos et al. (2024)
	Moreover, parasites can manipulate their host's odours, enhancing their attractiveness to vectors and thereby increasing their transmission success	O'shea et al. (2002), Díez-Fernández et al. (2020) and Silva et al. (2024)
Visual	Colour: Mosquitoes and sandflies have compound eyes containing photoreceptors sensitive to different wavelengths of light. Some mosquito and sandflies species are often more attractive darker colours with long-wavelength bands like orange, black, blue, purple and red than lighter colours. Blue, green and red light sources are highly attractive to sandflies	Brazil (2003), Jung et al. (2021), Wilson et al. (2021), Alonso San Alberto et al. (2022) and de Felipe et al. (2023)
Physical	Size: Different mosquito and sandfly species have varying levels of attraction to size. Some, like the *Aedes aegypti*, readily target humans regardless of size, whereas others, like *Anopheles* coluzzii and *Culex pipiens*, might show a stronger preference for larger animals like cows or horses. Larger animals often emit more of chemical cues and heat. Also for humans, age, gender, hormones, composition of skin and odour profiles are also affected the host preference. Other factors like shape and movement can also play a role in attracting mosquitoes	Carnaghi et al. (2024) and Coutinho-Abreu et al. (2022)
	Thermal stimuli: Mosquitoes and sandflies have specialized sensory organs called antennal pits located on their antennae. These pits contain heat-sensitive neurons that respond to changes in temperature. It allows them to locate warm-blooded hosts like humans and animals. Sensitivity to heat can vary among different mosquito species	Van Breugel et al. (2015), Zermoglio et al. (2017) and Greppi et al. (2020)

(OEH) and insulin-like peptides (ILPs) from the brain, initiating yolk production (Roy et al., 2016; Valzania et al., 2019). Specific ILPs, like ILP3, interact with distinct but related receptor tyrosine kinases: the insulin receptor (IR) and the OEH receptor (OEHR). Ligand binding (OEH and ILP3) activates IR and OEHR on the ovarian membrane, promoting follicle cell proliferation and nurse cell endoreplication (Roy et al., 2016). Notably, OEH potently stimulates ecdysteroid hormone production, primarily ecdysone (ECD), by the follicle cells (Brown et al., 2008; Dhara et al., 2013; Roy et al., 2016). In contrast, ILP3 appears crucial for midgut trypsin enzyme expression, facilitating bloodmeal digestion (Valzania et al., 2019). ECD from follicle cells is converted to 20-hydroxyecdysone (20E) by fat body adipocytes. Together with nutrient signalling via the rapamycin (TOR) pathway, this stimulates vitellogenin and other yolk component synthesis. Upon completion of yolk uptake and chorion deposition, mature eggs are formed (Kiesow and Pradel, 2016; Hansen et al., 2014). Little information about the development of eggs in sandflies could be found in the literature. A significant challenge in investigating the reproductive strategies of sandflies lies in the difficulty of acquiring females engorged with blood after feeding and unlike mosquito species that can be readily maintained through multiple blood-feeding cycles in laboratory colonies, rearing large sand fly colonies proves problematic due to their high mortality rates following the initial blood meal (Moraes et al., 2018).

Sandflies and mosquitoes have a broad host range, meaning they can feed on a variety of vertebrate animals, including humans, livestock (cattle, sheep etc.), rodents and even reptiles. Both insects generally prefer to bite any exposed skin, this includes the face, arms, hands, feet and legs for humans. Some mosquitoes can target specific body regions like ankle and feet with strong odours (Mponzi et al., 2022; Verhulst et al., 2016). Common bite sites for sandflies on other animal hosts include the nose, eyes, tail and undersides. These areas might be targeted because they offer easier access for the flies' mouthparts and potentially have thinner skin or fur, making them less sensitive to the initial bite itself. However, the delayed onset of pain, variation in sand fly species (some might have more potent saliva) and individual sensitivity can all contribute to differing experiences of sand fly bites.

These bites can be painless for some but quite noticeable for others, especially compared to mosquito bites (Munstermann, 2019). Warburg et al. (1994) observed a gradient in the intensity of the erythema response on volunteers bit by *Lutzomyia longipalpis* s.l. Bites inflicted by sandflies from the Brazilian colony elicited the strongest response, followed by those from Colombia. The Costa Rican sandflies induced the weakest erythema. A positive correlation was demonstrated between the size of the erythema caused by the bites and the levels of maxadilan, a vasodilatory peptide in sandfly saliva. Depending on species, sandflies are most active at dawn and dusk, seeking out blood meals during these periods. Their activity can be significantly reduced by factors like wind and rain (Kasap et al., 2009; Aklilu et al., 2017).

Frequent feeding habit (every 2–4 days for mosquitoes and 3–6 days for sandflies) makes them efficient vectors for various pathogens as host blood can potentially harbour pathogenic organisms. The blood they ingest, rich in protein (mainly haemoglobin), undergoes a fascinating two-stage digestive process within their gut, lasting 2–5 days. Volume of blood ingested can impact egg quality and quantity (Cecílio et al., 2022; Hawkes & Hopkins, 2021; Robert & Debboun, 2020). First, these insects act like a quality control inspector. Ingestion of a blood meal triggers the midgut to produce and secrete a diverse array of digestive enzymes such as trypsin, chymotrypsin, aminopeptidase and carboxypeptidase. These enzymes swiftly break down a small portion of blood proteins into smaller components, specifically peptides and amino acids. These breakdown products serve as vital nutritional. This initial digestion provides the insect with nutritional feedback and generates free amino acids as signals (Borovsky, 2003; Sanders et al., 2003; Telleria et al., 2010). If the blood quality passes the test, the mosquito and sandfly commit to a full-scale breakdown, ramping up enzyme production. These free amino acids act as key indicators, influencing the mosquito's decision to retain the meal and invest in further digestion (Martin-Martin et al., 2023). This two-stage process is crucial not only for the insect's nutritional needs but also for the survival and multiplication of pathogens within its system. Excess water from the blood meal is expelled through diuresis, allowing the mosquito to fly again and regulate body temperature. Both retaining the blood meal and producing large quantities of enzymes create an environment favourable for pathogen establishment and spread. Interestingly, feeding behaviour among mosquitoes varies greatly, with some species being generalists, whereas others show distinct preferences influenced by factors like season, hunger, dehydration and so on (Stein et al., 2013; Takken & Verhulst, 2013; Janousek et al., 2014; Hagan et al., 2018; Bouafou et al., 2024). Understanding these complexities is crucial in combating mosquito-borne diseases.

Following blood digestion, females undergo a gonotrophic cycle, culminating in the deposition of 30–60 eggs for sandflies and 30–300 eggs for mosquitoes. Sandflies favour dark, natural cavities such as rodent burrows, tree hollows, stone walls and rock crevices for daytime resting, these refugia are often situated within or around human dwellings and animal shelters (Cecílio et al., 2022). Mosquitoes prefer natural habitats that include dense vegetation, animal burrows, caves and tree holes or manmade structures such as basements, stables, chicken coops and culverts (Sauer et al., 2022) and females oviposit on or in water or on moist substrates or soil (Service, 2012). Sandfly eggs are oviposited in dark, humid environments with moist organic-rich soil. This rainforest floors, under rocks or decaying leaves, contaminated animal shelter soil. Some species like *Phlebotomus celiae*, *Ph. martini*, *Ph. longipes*, *Ph.pedifer*, *Ph.argentipes*, *Ph. chinensis* and *Ph. papatasi* are adaptable and can breed in diverse environments such as rodent burrows, caves and rock crevices, termite hill and even human dwellings (earthen floors) (Feliciangeli, 2004; Müller et al., 2011). This predilection for concealed oviposition sites contributes to the difficulty of locating immature stages in natural settings (Cecílio et al., 2022; Moncaz et al., 2012, 2014).

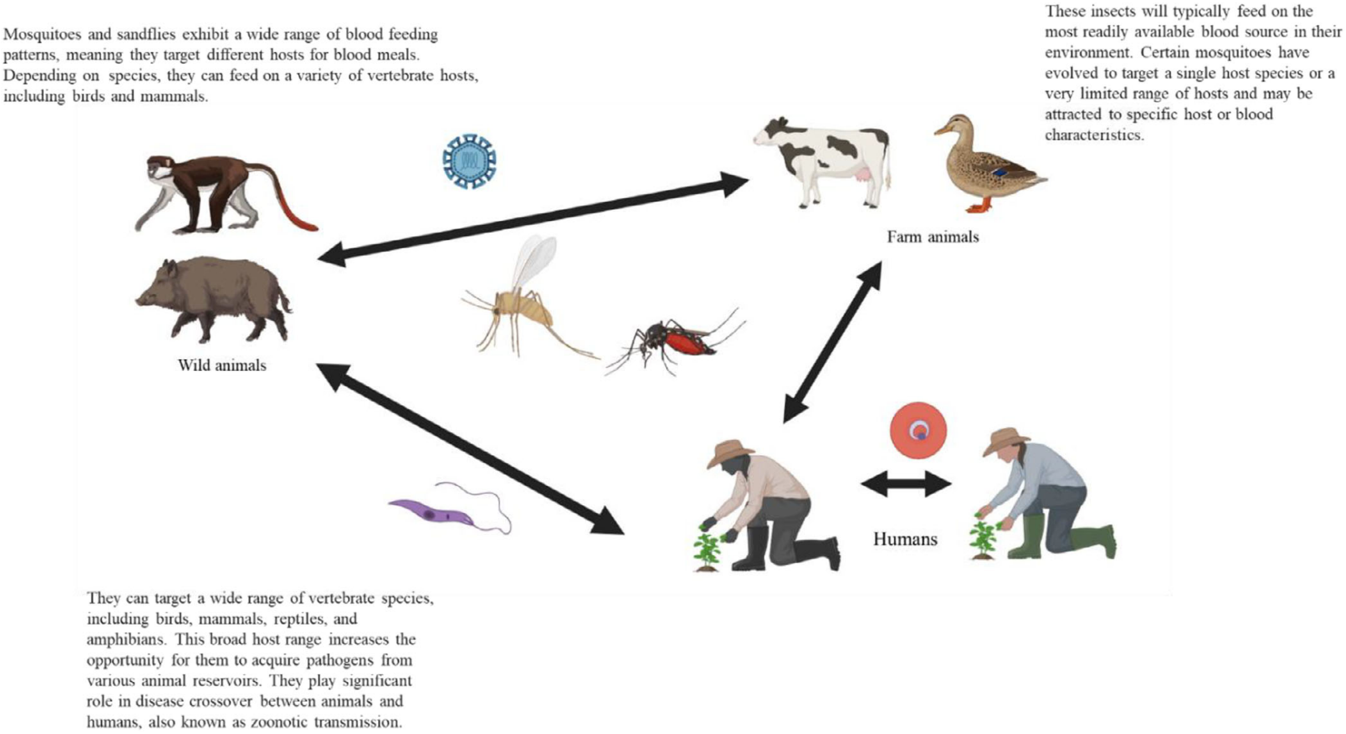
3 | EVOLUTIONARY ORIGINS OF BLOOD-FEEDING

Although these insects are undeniably associated with blood-feeding, their dietary habits exhibit surprising diversity (Fikrig & Harrington, 2021). Despite the ubiquitous image of females seeking blood meals, both sexes almost exclusively rely on sugar sources like flowers, fruits and honeydew for essential physiological functions. This readily available nectar fuels flight, reproduction and overall maintenance, establishing it as their dominant food source. However, blood meals become pivotal for female sandflies and mosquitoes solely during egg production (Foster & Walker, 2019) (Figure 1). Interestingly, a small subset of female species defies this convention, entirely relying on nectar and sugary sources akin to their male counterparts. Examples include the *Toxorhynchites* genus, where both sexes feed solely on nectar, and the *Malaya* genus, known for their unique method of acquiring regurgitated food from ants (Clements, 1999; Day, 2005; Steffan & Evenhuis, 1981).

The evolutionary origins of blood-feeding in insects propose two distinct pathways:

1. Accidental exploitation: This suggests a shift in resource utilization, where plant-sucking insects inadvertently bit vertebrates and subsequently developed a digestive system capable of processing the blood's rich protein content (Waage, 1979). Chance encounters and subsequent physiological adaptations drove this transition.
2. Gradual transition: Alternatively, chewing insects might have developed a closer association with vertebrates, adapting to specific host cues and occasionally feeding on their skin (Lehane, 2005). Over time, this could have led to a complete reliance on blood, triggering co-evolutionary arms races between host and parasite.

In both scenarios, the evolving insects became increasingly dependent on host-specific cues for efficient identification and resource acquisition within diverse environments. This reliance ultimately led to the evolution of host preference; an adaptive trait crucial for maximizing the reproductive fitness of these parasitic insects (Lyimo & Ferguson, 2009). Blood feeding has evolved independently in multiple insect lineages, including mosquitoes, sandflies, bed bugs, midges and lice. This exemplifies convergent evolution, where similar adaptations



Mosquitoes and sandflies exhibit a wide range of blood feeding patterns, meaning they target different hosts for blood meals. Depending on species, they can feed on a variety of vertebrate hosts, including birds and mammals.

These insects will typically feed on the most readily available blood source in their environment. Certain mosquitoes have evolved to target a single host species or a very limited range of hosts and may be attracted to specific host or blood characteristics.

They can target a wide range of vertebrate species, including birds, mammals, reptiles, and amphibians. This broad host range increases the opportunity for them to acquire pathogens from various animal reservoirs. They play significant role in disease crossover between animals and humans, also known as zoonotic transmission.

FIGURE 1 The blood feeding pattern of sandflies and mosquitoes and the potential zoonotic disease transmission routes of important blood-borne pathogens including arboviruses, *Leishmania* and *Plasmodium*.

arise due to similar selection pressures (Arcà & Ribeiro, 2018; Freitas & Nery, 2020; Henriques et al., 2017). Comparative functional genomics studies reveal functional convergence related to hematophagy. Specifically, certain distinct proteins found in salivary glands have the same function across these lineages. For instance, lipocalins and D7 proteins act as biogenic amine scavengers in ticks, kissing bugs and mosquitoes (Calvo et al., 2006). Furthermore, four gene families have been shown to be differentially expressed in blood-feeding insects compared to their non-blood-feeding counterparts. Two of these families exhibit rapid expansions in blood-feeding lineages: small heat shock protein HSP20, this expansion might be a case of convergent evolution due to its presence in a non-blood-feeding ancestor; and carboxylesterase, the function of this expansion remains unclear. Conversely, two other gene families show rapid contractions in blood-feeding lineages: Transmembrane protein, the function of this contraction is unclear; and odorant-binding protein, this contraction might be linked to a reduced reliance on odour cues in a blood-feeding lifestyle (Freitas & Nery, 2020).

New research suggests the emergence of blood feeding in mosquitoes has a much older origin. Soghigian et al. (2023) employed phylogenomic analysis of 709 single-copy ortholog groups across 256 mosquito species. This investigation unveils a considerably older emergence for mosquitoes than previously estimated, placing their origins in the early Triassic period, approximately 217 million years ago. Furthermore, the analysis suggests that the transition to feeding on mammalian blood has occurred independently multiple times within distinct mosquito lineages. This finding challenges the notion of blood feeding as a singular ancestral trait, instead indicating its repeated acquisition and loss throughout insect evolution. Additionally, the diversification of mosquito lineages appears to be linked to two significant historical events: the diversification of vertebrate classes (mammals, birds etc.) throughout Earth's history. This suggests a potential co-evolutionary dynamic between mosquito evolution and the emergence of novel blood sources and the fragmentation of ancient supercontinents may have created new ecological niches, thereby facilitating opportunities for mosquito radiation (diversification).

Building upon the established existence of genetic variation in mosquito host preference, further inquiry is required to elucidate the selective pressures favouring anthropophagy (feeding on humans). Natural selection favours traits that enhance fitness. However, the specific benefits of human blood feeding remain unclear. Humans, as large, relatively immobile, and densely populated mammals, present a readily available blood source for insects. Their limited ability to swat away feeding mosquitoes further simplifies blood acquisition. Human blood might offer a more suitable or abundant protein source compared to the blood of other animals, directly impacting mosquito egg development and overall reproductive success. Mosquitoes specializing on humans might experience lower predation pressure. Humans, while actively swatting at mosquitoes, might be less effective against those specifically adapted to feed on them, ultimately enhancing their survival rates. Rose et al. (2020) investigated the origin and potential future trajectory of mosquito preference for human blood in sub-Saharan Africa, a region with a high burden of mosquito-borne diseases. They found a significant variation in the preference for human blood among *Ae. aegypti* mosquitoes collected from 27 geographically diverse locations across sub-Saharan Africa. Statistical modelling linked over 80% of this behavioural variation to two key ecological factors: Areas with harsher dry seasons likely favoured mosquitoes that could exploit human-stored water for breeding, leading to increased contact with humans, and higher human density offered more readily available blood sources, potentially selecting for mosquitoes that readily fed on humans. Whole-genome sequencing of 375 mosquitoes revealed a single ancestral component associated with the preference for human blood. This suggests a single evolutionary origin for this behaviour. Interestingly, genetic changes associated with human-feeding tendencies were concentrated in specific chromosomal regions, indicating potential hotspots for future research. The study proposed that human blood feeding likely emerged as an adaptation for survival during harsh dry seasons. Mosquitoes that utilized human-stored water for breeding would have had more frequent contact with humans, making the switch to human blood an advantageous by product (Rose et al., 2020).

By delving deeper into insect biology, behaviour and sensory perception, we gain valuable insights into their role in disease transmission. This knowledge empowers us to develop effective control strategies and combat the global burden of vector-borne illnesses.

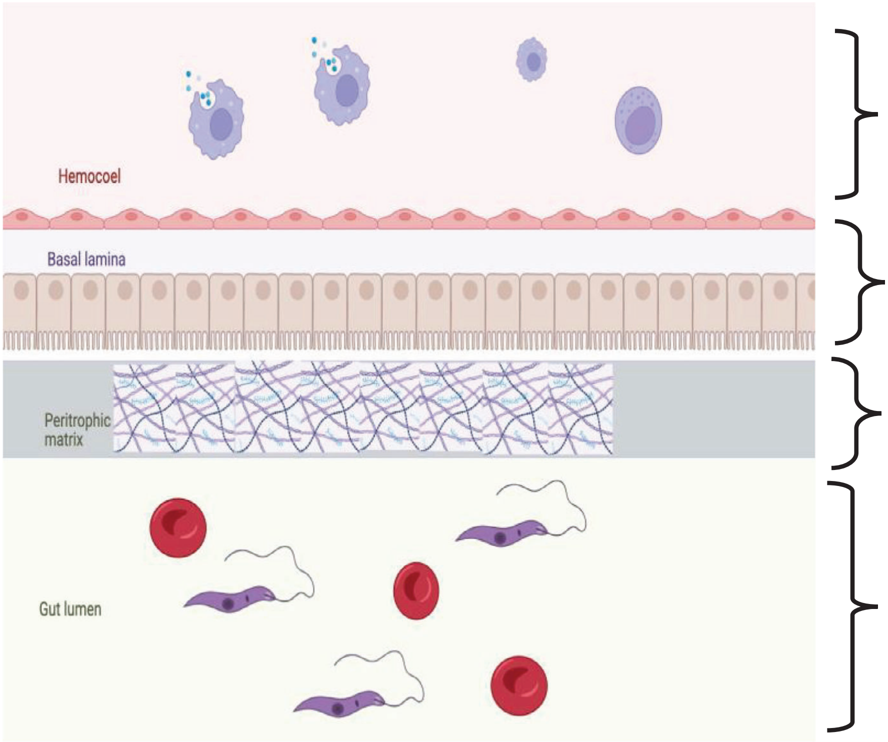
4 | MOSQUITO AND SANDFLY DEFENCE AGAINST BLOOD-BORNE PATHOGENS

Vector-borne pathogens navigate a specific route within their host insect: midgut (where they enter with the blood meal), hemocoel (main blood cavity) and salivary glands (where they end up being injected into a new host) as they attempt to complete an obligate migration across the insect host. Blood source (human, animal and wildlife) can influence transmission due to the presence of different pathogens or blood factors like haem affecting pathogen survival (Beerntsen et al., 2000; Carvajal-Lago et al., 2021; Valkiunas, 2004). The type of blood these insects ingest can influence the transmission of these pathogens in several ways. Different blood sources (humans, livestock and wildlife) may harbour different pathogens, increasing the risk of transmission for certain diseases (Ellwanger & Chies, 2021) (Figure 1). Moreover, the blood quality and immune factors such as haem present can affect the pathogen's survival and multiplication within the mosquito/sandfly, impacting transmission efficiency (Gabrieli et al., 2021).

Vector competence, defined as the ability to transmit pathogens, is a multifaceted trait shaped by environmental, behavioural and genetic factors of the mosquito/sandfly species. Notably, genetic variation in immune effector molecules significantly impacts vector competence (Azar & Weaver, 2019) (Figure 2). Following ingestion of an infected blood meal, mosquitoes and sandflies employ a multifaceted immune arsenal to combat blood-borne pathogens (Bartholomay & Michel, 2018; Rossi et al., 2015; Souza-Neto et al., 2019). The regulation of pathogen infection in these insects involves physical and physiological barriers to prevent pathogen entry and establishment, followed by a coordinated interplay between cellular and humoural immune responses if entry occurs (Elrefaey et al., 2021; Yu et al., 2022).

Blood-engorged insects possess a type I peritrophic matrix, which is composed of chitin, proteins and proteoglycans within their midgut. This semi-permeable structure serves a multifaceted protective role: (i) safeguarding the midgut microvilli from potential damage inflicted by the concentrated digestive enzymes, (ii) mitigating the detrimental effects of haem, a byproduct of blood digestion and (iii) acting as a barrier against invading pathogens (Secundino et al., 2005) (Figure 2). Parasites must overcome this intricate structure as well as resist the effects of digestive proteases to establish a successful infection within the insect host. For instance, following blood meal ingestion (approximately 48 h), infectious *Leishmania* (procyclic promastigote stage) and *Plasmodium* (intraerythrocytic gametocytes) parasites produce enzymes such as proteases and chitinases that target the integrity of the peritrophic matrix (Li et al., 2010) and transition from rapid replication to a motile developmental form. This motile form facilitates escape from the peritrophic matrix and establishes itself within the midgut lumen. Significantly, this motile stage also mediates attachment to the sand fly or mosquito midgut, a critical step for *Leishmania* and *Plasmodium* parasite life cycles within the insect vector. This attachment prevents parasite elimination alongside residual blood meal components during defecation (Dostálová & Volf, 2012; Bennink et al., 2016).

Some parasites/pathogens especially viruses must first penetrate the midgut epithelium, the layer of cells lining the midgut. Successful penetration establishes an infection within these cells before the pathogens can migrate and potentially enter the hemocoel. This systemic invasion could then lead to the colonization of the salivary glands, a crucial step for transmission to new vertebrate hosts (Franz et al., 2015). Some pathogens like *Plasmodium* might embed themselves in the space between the midgut endothelium and basal lamina and mature as cysts over an extended period before producing forms that migrate to the salivary glands of the mosquito (Smith et al., 2014). Here, these parasites are impacted by the cellular and humoural responses of the insect midgut epithelium or hemocoel. The innate response aims to limit pathogen replication through phagocytosis, melanization and lysis, triggered by diverse signalling pathways within the insect-pathogen interaction (Keleta et al., 2021; Ratcliffe et al., 2024). In essence, mosquitoes and sandflies rely on their innate immune system to combat invading pathogens. The initial step involves the recognition and binding of invading pathogens by pattern recognition receptors (PRRs) on the host surface. These PRRs specifically target pathogen-associated molecular patterns displayed by the pathogens. This recognition event triggers the activation of various immune signalling pathways within insects, ultimately leading to the deployment of cellular and humoural immune responses (Hillyer & Strand, 2014). Cellular immunity functions in the hemolymph, the insect equivalent of blood, to defend against pathogen invasion. Hemocytes and pericardial cells, specialized immune cells, mediate phagocytosis and encapsulation responses, directly eliminating or isolating the pathogens (Hillyer & Strand, 2014). Humoural immunity, also operating within the hemolymph, encompasses a broader range of defence



Hemocoel habors hemocytes and pericardial cells, specialized immune cells, mediate phagocytosis and encapsulation responses, directly eliminating or isolating the pathogens

Midgut epithelium

Peritrophic matrix is a semi-permeable that safeguards the midgut microvilli from potential damage inflicted by the concentrated digestive enzymes, (ii) mitigates the detrimental effects of heme, a byproduct of blood digestion, and (iii) acts as a barrier against invading pathogens

Midgut

FIGURE 2 The interaction of blood-borne pathogens with insect host's physical and physiological barriers.

mechanisms. Hemocytes, the insect equivalent of macrophages, directly combat pathogens through phagocytosis and indirectly contribute to defence by secreting various effector molecules. These effectors include antimicrobial peptides (AMPs), complement-like proteins with direct microbicidal activity against pathogens, and factors that mediate the melanization response (Cardoso-Jaime et al., 2022; Sigle & Hillyer, 2016). Additionally, the phenoloxidase (PO) cascade is activated, leading to melanization, a process that encapsulates and inactivates pathogens. Finally, the production of reactive oxygen species (ROS) and nitric oxide contributes to the antimicrobial arsenal employed by the insect humoural immune system (Hillyer & Strand, 2014). Also, regulating gut microbiota can alter immunological responses, greatly influencing their capacity as vectors.

The mosquito's immune system might react differently to blood from different sources, potentially inhibiting or enhancing pathogen transmission (Gabrieli et al., 2021; Kumar et al., 2018; Yu et al., 2022). Notably, transcriptome-wide analyses across diverse mosquito species revealed a remarkable overlap in immune response genes activated against various pathogen classes (Bartholomay et al., 2010). Pattern recognition molecules, production of AMPs and generation of ROS and reactive nitrogen species (RNS) are thought to be key players in both the epithelial and systemic immune responses against parasitic infections like *Leishmania* and *Plasmodium*. These immune responses ultimately determine vector susceptibility to these pathogens. Interestingly, studies comparing different mosquito-*Plasmodium* combinations revealed significant variations in epithelial RNS/ROS responses (Molina-Cruz et al., 2012, 2013). These findings suggest that the ongoing 'evolutionary arms race' exists between parasites and their vectors. Parasites have developed mechanisms such as modifications of cell surfaces to evade their susceptible host's immune system (not discussed here), whereas the insect immune system can adapt its response depending on the specific blood source or parasite encountered (Caljon et al., 2016; Schmid-Hempel, 2021). These evasion strategies might involve manipulating the host's immune system by either disrupting self-recognition mechanisms or suppressing the induction or effector functions of the host's defence pathways. For instance, parasites must contend with ROS, a critical component of the antimicrobial defence system in both invertebrate and vertebrate hosts. In insects, dual oxidase plays a pivotal role in infection-induced hydrogen peroxide production, a substrate for various peroxidases. This enzyme is tightly regulated at the transcriptional and post-translational levels, allowing for maintenance of basal ROS levels under normal conditions and upregulation of ROS production in response to an increased bacterial load within the gut (Charroux & Royet, 2012; Diaz-Albiter et al., 2012). ROS can exert direct antimicrobial effects and additionally activate the Toll pathway, further amplifying the immune response by stimulating the production of AMPs (Pan et al., 2012). Studies have shown significant increases in oxidative responses within disease vectors upon pathogen exposure. Conversely, the presence of antioxidants that scavenge ROS or silencing of detoxifying enzymes can exacerbate pathogen establishment in the invertebrate host. This phenomenon is thought to be linked to the activation of the PO cascade, potentially triggered by increased pathogen proliferation within the insect (Diaz-Albiter et al., 2011; Kumar et al., 2003; Molina-Cruz et al., 2008).

Similarly, sandflies possess a functional innate immune system that can be activated in response to parasite infection. This immune response involves the activation of various signalling pathways and the upregulation of immune factors like AMPs, which help to combat the parasite. A considerable body of research exists on the response of mosquito/sandfly innate immunity to parasite transmission success (Dostálová & Volf, 2012; Kykalová et al., 2021). Dillon et al. (2006) identified putative immune proteins identified using expressed sequence tag analysis of a whole-body cDNA library from *L. longipalpis* sandflies, both infected and uninfected with *Leishmania infantum*. These proteins included Gram-negative binding proteins, galectins, thioester proteins, scavenger receptors, signalling pathway components, serpins, caspases and peroxidases and are involved in gut barrier function, digestive processes and the immune response against invading parasites like *Leishmania*. Telleria et al. (2018) demonstrated changes in immune gene expression following *Leishmania* infection. These changes in immune gene expression activated Toll, Imd and JNK pathways, as well as antioxidant enzymes like catalase, glutathione *S*-transferase, superoxide dismutase and peroxiredoxin, responsible for regulating ROS levels (Telleria et al., 2021). Additionally, studies show upregulation of Dorsal and Relish genes, known positive regulators of the Toll and Imd pathways, respectively, following *Leishmania* challenge, leads to increased expression of AMPs such as attacin, cecropin and defensin 2 in the sandfly LL5 cell line at different time points (Tinoco-Nunes et al., 2016).

5 | HOW DO MOSQUITO AND SANDFLY FIND HOSTS? THE POWER OF SMELL

Mosquitoes and sandflies navigate their world and fulfil crucial tasks like host-seeking and egg-laying primarily through their remarkable sense of smell (Table 2 and 3). This sophisticated olfactory system relies on specialized organs like antennae, maxillary palps and the proboscis (Wolff & Riffell, 2018; Wheelwright et al., 2021). These organs are packed with diverse olfactory receptors (ORs) that act as translators, converting airborne odour molecules into nerve signals that guide insect behaviour (Wang et al., 2010; Leal, 2013). Interestingly, the structure of these organs can vary across species and even between sexes within the same species (Wolff & Riffell, 2018).

What's most fascinating about mosquito and sandfly olfaction is its primacy in host seeking. These tiny insects first use chemical cues detected through their smell to locate potential blood meals (Takken & Knols, 1999; Potter, 2014). This reliance on smell is not unique to these insects; it is deeply conserved across insects and even transcends the divide between vertebrates and invertebrates, suggesting a fundamental similarity in how different animals perceive and respond to odours. The magic of smell happens within hair-like structures called sensilla, predominantly found on the antennae and maxillary palps. Compared to other senses like vision, the sense of smell mediated by the antennae plays a dominant role in the life of these insects. It has a vast number of sensilla (Clements, 2023). These sensory outposts house the ORs, the 'detectives' tasked with identifying odour molecules. Odour molecules first enter the sensilla through tiny pores in the exoskeleton. Once inside, odorant-binding proteins act as carriers, transporting these molecules through the hemolymph to the waiting ORs (Wang et al., 2010; Leal, 2013). The number of ORs varies significantly across insect species, ranging from 79 in the *Anopheles gambiae* to a whopping 177 in the *Culex quinquefasciatus*, suggesting intriguing differences in their olfactory capabilities (Bohbot et al., 2007; Leal, 2013; Zhou, Yang, et al., 2014). *L. longipalpis* sandfly has a more diverse olfactory system with a higher number of sensilla subtypes (11) (Fernandes et al., 2008) compared to *Nyssomyia intermedia*, which has six (Fernandes et al., 2020).

The sensilla on these antennae equips them with an exceptional sense of smell, making it an irreplaceable tool for their survival and reproduction. Nectar, a vital energy source for adult mosquitoes, is tracked using olfactory cues (Nyasembe, 2017). Moreover, these insects meticulously choose oviposition sites to optimize offspring survival, guided by complex interactions between environmental factors and sensory cues (Baik & Carlson, 2020; Girard et al., 2021). This process of meticulous oviposition site selection highlights the fastidious behaviour of gravid females. This behaviour is likely driven by the need to optimize offspring survival. Furthermore, perhaps the most concerning aspect of mosquito and sandfly olfaction is their ability to locate and target human and animals for blood meals. Research has identified several host-derived attractants, including lactic acid (present in sweat and breath), 1-octen-3-ol (found in sweat and breath) and carbon dioxide (exhaled at high concentrations) (Hill et al., 2015; Müller et al., 2015; Majeed et al., 2016). Notably, wind tunnel and olfactometer studies suggest host volatiles can act as kairomones for mosquito species, with lactic and carboxylic acids identified as potential attractants. Field studies, particularly with *An. gambiae* and *Cx. quinquefasciatus*, corroborate these findings, demonstrating the long-distance attraction of these mosquitoes to human volatiles (Zwiebel & Takken, 2004). As described previously, mosquitoes and sandflies can detect a diverse array of volatile organic compounds (VOCs) emitted by potential hosts and their environments. Notably, specific VOCs, like 6-methyl-5-hepten-2-one, α-pinene, hexanoic acid, benzyl alcohol, m-cresol, p-cresol and decanal, may hold particular appeal to a wider range of these insects, influencing their behaviour in seeking breeding grounds, resting areas or blood meals (Bray & Hamilton, 2007; Bezerra-Santos et al., 2024; Hassaballa et al., 2021; Tavares et al., 2018; Wooding et al., 2020). A recent study (Zhou, Deng et al., 2023) investigated the impact of antenna damage on mosquito behaviour and how much antenna a mosquito needs to smell a host. They observed that mosquitoes locate hosts even with an incomplete antenna but the 6th and 7th segments of the *Ae. albopictus* mosquito antenna are crucial for host detection. This suggests a protection/compensation mechanism within the antenna. Parasite infection can potentially modify host odours, inducing changes in breath volatiles and/or those associated with the epidermal microbial flora. Notably, such alterations may enhance the attractiveness of infected hosts to mosquito and sandfly vectors (Díez-Fernández et al., 2020; O'shea et al., 2002; Silva et al., 2024).

Beyond olfaction, these insects integrate other sensory inputs. Visual characteristics like host colour, surface texture and surrounding vegetation influence decisions regarding host and breeding site

TABLE 2 Some important mosquito species and their host seeking behaviour.

Species	Distribution and invasive potential	Host preference	Blood feeding location preference	Resting preference	Number of bloodmeals per gonotrophic cycle	Transmitted diseases	References
Aedes aegypti	Invasive	Anthropophilic	Endophagic	Endophilic	Multiple	Dengue fever, chikungunya, zika fever and yellow fever virus	Mann et al. (2020) and Sene et al., 2022)
Aedes albopictus	Invasive	Opportunistic and generalist zoophilic (humans, domestic and wild animals, reptiles, birds and amphibians)	Exophagic	Exophilic	Multiple	Yellow fever virus, dengue fever, chikungunya fever and several filarial nematodes	Shirai et al. (2004), Prasadini et al. (2019) and Bursali and Şimşek (2023)
Aedes japonicus	Forest areas in Asia and Europe; invasive	Mammals	Exophagic and endophagic	Exophilic	Two	Japanese encephalitis virus	Kaufman and Fonseca (2014)
Aedes koreicus	Invasive (Japan, north-eastern China, South Korea and southern Russia)	Opportunistic (highly anthropophilic)	Endophagic	Endophilic	Multiple	Japanese encephalitis virus	Ganassi et al. (2022)
Anopheles funestus	Africa	Anthropophilic	Endophagic	Endophilic	Two	*Plasmodium falciparum* – malaria	Mbewe et al. (2022)
Anopheles sacharovi	Coastal parts of Mediterranean Europe	Humans and cattle	Exophagic and endophagic	Endophilic	Multiple	*Plasmodium vivax* – malaria	Ngom et al. (2013), Bursali and Şimşek (2022) and Gueye et al. (2023)
Anopheles stephensi	Indian subcontinent, East and South Asia, Africa	Anthropophilic	Endophilic and endophagic	Endophilic	Multiple	Bovine leukemia virus – and *Plasmodium berghei, falciparum and vivax*	Thomas et al. (2017) and Briggs et al. (2022)
Anopheles gambiae	Africa	Anthropophilic	Endophagic	Endophilic	Two	*Plasmodium falciparum* – malaria	Lyimo et al. (2012) and Mbewe et al. (2022)
Culex tritaeniorhychus	Southeast Asia, the Middle East, Africa and Europe	Cows, pigs, occasionally on humans	Exophagic and endophagic	Exophilic	Two	Japanese encephalitis virus	Bursali and Şimşek (2022) and Guta et al. (2021)
Culex pipiens	Widely distributed Europe, Africa and Asia	Ornithophilic	Exophagic	Exophilic	Two	West Nile and Usutu Viruses, Canine dirofilarial worms and avian malaria parasites	Gomes et al. (2001), Bursali and Şimşek (2022) and Guta et al. (2021)
Culex quinquefasciatus	Subtropical and tropical areas worldwide	Opportunistic (mammals and/or birds)	Exophagic	Exophilic	Multiple	St. Louis encephalitis virus, Western equine encephalitis virus, zika virus and West Nile virus	Muturi et al. (2008)

TABLE 3 Some important sandfly species and their host seeking behaviour.

Species	Distribution	Host preference	Blood feeding location preference	Resting preference	Transmitted diseases	References
Phlebotomus perniciosus	Western Europe (Portugal, Spain and France), northern Africa, Italy, Malta and Balkan countries	Opportunistic (mammals and/or birds)	Endophagic	Endophilic	*Leishmania infantum*, *Leishmania tropica* and Toscana virus	De Colmenares et al. (1995), Martín-Martín et al. (2015), Abbate et al. (2020), Pérez-Cutillas et al. (2020) and Messahel et al. (2022)
Phlebotomus ariasi	Western Europe (Portugal, Spain and France), northern Africa	Horse, cows and chicken	Endophagic	Endophilic	*L. infantum*	Guy et al. (1984), Maia et al. (2013) and Pérez-Cutillas et al. (2020)
Phlebotomus orientalis	Africa	Opportunistic (especially mammals)	Endophagic	Endophilic	*Leishmania donovani*	Yared et al. (2015, 2019), Gebresilassie et al. (2015) and Jibreel et al. (2023)
Phlebotomus papatasi	Western Europe (Portugal, Spain and France), northern Africa, Italy, Malta and Balkan countries	Mammals	Endophagic	Endophilic	*Leishmania major*	Zivkovic et al. (1971), Bongiorno et al. (2003), Abedi-Astaneh et al. (2015), Pérez-Cutillas et al. (2020) and Yared et al. (2019)
Phlebotomus argentipes	Southeast Asia Region	Opportunistic (humans, dogs and cattle)	Endophagic	Endophilic	*L. donovani*	Dinesh et al. (2001), Kushwaha et al. (2022), Bern et al. (2010) and Garlapati et al. (2012)
Phlebotomus sergenti	Europe, northern Africa, Southern America and Balkan countries	Mammals/chicken	Endophagic	Endophilic	*L. tropica* and Toscana virus	Bongiorno et al. (2003), Maia et al. (2013) and Abbate et al. (2020)
Phlebotomus perfilewi	Europe	Livestock and humans	Endophagic	Endophilic	*L. infantum*	Bongiorno et al. (2003)
Phlebotomus tobbi	Balkan Peninsula, in Greece, the Middle East and Turkey	Mammals	Endophagic	Endophilic	*L. infantum*/*L. donovani* hybrids	Svobodová et al. (2009), Seblova et al. (2015) and Vaselek and Volf (2019)
Phlebotomus similis	Balkan Peninsula, in Greece, the Middle East and Türkiye.	Anthropophilic	Endophagic	Endophilic	*L. donovani*, *L. major and L. tropica*	Maroli et al. (2013)
Phlebotomus mascitii	France, Belgium and Germany, to the west in north-eastern Spain, and is endemic in some Balkan countries, Greece, Türkiye and central European countries	Chicken/equine	Endophagic	Endophilic	*L. infantum*	Kniha et al. (2020)
Lutzomyia longipalpis	Central and South America	Mainly anthropophilic but feed from animals, livestock and wildlife	Lacks a pronounced indoor/outdoor feeding preference	Lacks a pronounced indoor/outdoor feeding preference	*L. infantum*	Silva Sales et al. (2015), de Sousa-Paula et al. (2020) and Retkute et al. (2021)
Lutzomyia evansi	Central and South America	Zoophilic (can feed on humans)	Exophillic	Exophillic	*L. infantum*	Paternina et al. (2016) and Mejía et al. (2018)
Nyssomyia neivai	South America	Opportunistic	Exophillic	Exophillic	*Leishmania* spp.	Galati et al. (2009) and Copa et al. (2021)

selection (Parker et al., 2020; Baik & Carlson, 2020). Less extensively studied, gustatory and tactile cues also contribute to the final evaluation and selection of oviposition sites (Girard et al., 2021).

6 | BLOODSUCKING MOUTHPARTS AND FEEDING STRATEGIES

Their mouthparts are a marvel of adaptation that penetrates the host's skin (Zhou, Yang et al., 2023). Females also possess a paired salivary gland and a smaller medial lobe located in the thorax. Each gland is connected by a common duct and releases saliva containing anticoagulants and vasoactive proteins and enzymes like apyrase and hyaluronidase, which prevent blood clotting and facilitate feeding (Billingsley et al., 2006). Muscles within the proboscis pump the ingested blood, whereas maxillary palps act as sensory organs, monitoring blood flow and guiding further probing if necessary (Paige & Duvall, 2022). The feeding process, lasting several minutes, involves repeated skin probing until a blood vessel is located and pierced, enabling blood extraction. These insects possess sophisticated methods to circumvent the host's immune response during blood feeding. Their saliva also harbours substances that dilate blood vessels and prevent platelet aggregation following blood vessel damage, facilitating easier access to blood resources (Vogt et al., 2018). Additionally, various salivary components actively suppress inflammatory pathways and platelet aggregation, further impeding blood coagulation. These adaptations enable mosquitoes to feed undetected for extended periods, maximizing their potential for acquiring a blood meal and transmitting pathogens. Notably, saliva contains a diverse array of biochemical agents, including anticoagulants like heparin, found within the salivary glands, midgut and even the salivary canal of both male and female mosquitoes (Ha et al., 2014; Isawa et al., 2002; Nouzova et al., 2019).

Although mosquito and sandfly mouthparts are generally adapted for blood feeding across vertebrates, genetics, ecological niche and host availability are the factors that determine their specific blood-feeding preferences. These insect vectors demonstrate preferential host selection; this behaviour is not rigid. These organisms exhibit plasticity in their host choices, adapting their feeding strategies based on the availability of potential hosts and displaying opportunistic inclinations (Keven et al., 2017; Mbewe et al., 2022). This raises the question of whether feeding patterns are driven more by innate preferences for certain hosts or simply by the accessibility of available blood sources. Physiological limitations are another primary driver of blood-host choice.

Notably, research by Chaves et al. (2010) suggests an aggregated feeding pattern, where most species exploit the same vertebrate hosts, which likely reflects opportunistic exploitation of readily available blood sources. The specific effects of co-occurrence and aggregated feeding on disease transmission depend on a complex interaction of factors including the type of disease and its transmission dynamics, the competence of different mosquito/sandfly species as vectors for the disease and the density and distribution of infected hosts and susceptible vertebrate populations. There can be increased transmission rates. If multiple species target the same host, there will be a greater overall number of bites. This increases the chance of an infected insect transmitting a pathogen to the host compared to a scenario with only one mosquito/sandfly species feeding. For instance, multiple *Anopheles* mosquito species can feed on humans, and some, like *An. gambiae*, are efficient malaria vectors, so aggregated feeding by these species on humans can significantly increase malaria transmission rates in endemic areas (Takken et al., 2024). The establishment of infection in a host can vary depending on the vector and pathogen. Some vector-borne diseases necessitate inoculation of the pathogen through multiple bites from an infected insect (e.g. leishmaniasis transmitted by sandflies; Giraud et al., 2019), others, such as mosquito-borne diseases like dengue fever, can be typically transmitted with a single bite (Rückert et al., 2017). Aggregated feeding creates a situation where a single host might be bitten by several infected flies within a short period, potentially increasing the transmission success rate of the disease. It has been shown that compared to solitary feeders, sandflies that feed in groups exhibit decreased saliva expenditure, increased blood intake and an enhanced egg production. This cooperative feeding maximizes the effect of injected saliva, facilitating blood intake and suppressing host immune defences (Tripet et al., 2009).

Sandfly species like *Phlebotomus perniciosus* and *Sergentomyia minuta* can both feed on humans and animals. If these species co-occur in an area with *Leishmania* parasites, their aggregated feeding on infected animal reservoirs and humans can contribute to disease transmission. If one of the aggregated feeding species is not a natural vector for a particular disease but feeds on the same host as a known vector, it can potentially acquire the pathogen from the infected host and subsequently transmit it to another susceptible host, acting as a 'bridge' and expanding the potential host range of the disease. Aggregated feeding can create competition among mosquito/sandfly species for blood meals. This phenomenon may lead to frequent interruptions during feeding events. Due to the random arrival of individuals at the host site, each female experiences a constant threat of displacement by competitors. Furthermore, these interruptions might be size-dependent, with smaller females being more susceptible to dislodgement by larger rival (Kelly et al., 1996). Interestingly, a study on *Ae. albopictus* and *Ae. aegypti* housed together in insect cages found both species fed more frequently compared to solitary conditions, suggesting competition might drive more aggressive blood-seeking behaviour (Bursalı, 2024a). Furthermore, competition at feeding sites could potentially trigger increased defensive behaviours from the host (Terrill & Shultz, 2023). This could potentially favour the evolution of more virulent strains of pathogens within the infected insects. These strains can replicate faster and be transmitted more readily during the short feeding window available when multiple insects are targeting the same host.

7 | BLOOD FEEDING PATTERN

Mosquitoes and sandflies may exhibit varying degrees of selectivity for specific hosts, ranging from a broad spectrum of invertebrates and vertebrates to a more focused preference (Tables 2 and 3). The type of host blood meal can significantly impact the reproductive success (fecundity) of blood-feeding insects. Takken et al. (2002) demonstrated this in their study, where *An. gambiae* s.s. and *An.quadriannulatus* mosquitoes exhibited substantial differences in fecundity when fed human blood compared to cattle blood. Interestingly, research suggests a potential disconnect between preferred host and optimal reproductive output. For example, Lyimo et al. (2012) found that *An. gambiae* s.s. feeding on human blood, their preferred host, did not necessarily translate to higher fitness. Bursali and Şimşek (2023) investigated the influence of various blood sources (human, mouse, bird, cow and sheep) on the feeding behaviour and subsequent reproductive output of *Ae. aegypti* and *Ae. albopictus* mosquitoes within the artificial feeding system employed in a laboratory setting. Their findings confirmed that the chosen blood meal significantly impacts both feeding rates and subsequent egg, larvae and pupae production in *Ae. aegypti*. Notably, *Ae. aegypti* displayed a clear preference for bird blood, with the highest feeding rates observed on this blood source. In contrast, *Ae. albopictus* favoured mouse blood in this study (Bursali & Şimşek, 2023). These observations align with findings by Lyimo and Ferguson (2009), who reported that *Ae. aegypti*, another human-feeding mosquito, exhibited the highest fitness when fed on bird blood compared to blood types in controlled feeding experiments using artificial membranes (Bursali & Simsek, 2023; Prasadini et al., 2019). Notably, the type of blood did not influence their reproductive success. In another study, *Ae. albopictus* females also exhibited a higher landing frequency on the forearm of human volunteers with O blood than on other blood types (Shirai et al., 2004). The frequency and regularity of blood feeding can differ substantially between species, subsequently influencing disease transmission (Brackney et al., 2021). Mosquitoes can even detect and respond to blood sugar levels. *Ae. aegypti* mosquitoes prefer blood from non-diabetic individuals compared to diabetic individuals. This preference seems to be across all blood types with a range of 50%–65% favouring non-diabetic blood suggesting diabetic blood has different chemical cues or nutrient profiles that are less attractive to the mosquitoes (Bursalı, 2024b).

Field studies offer valuable insights into the diverse feeding patterns of mosquitoes and sandflies (Tables 2 and 3). For instance, Bursali and Şimşek (2022) employed multiplex PCR to analyse blood meals from wild-caught, blood-fed females of three mosquito species (*Cx. pipiens*, *An. sacharovi* and *Cx. tritaeniorhynchus*) in Türkiye (Aegean and Mediterranean regions, 2017–2019). Their findings revealed a strong preference for bovine blood across all three species, exceeding 86%. Human blood meals were significantly less frequent (<10%). Mosquitoes were collected from rural barns, houses and chicken coops. Similar results were obtained again from the same captured mosquito species from May 2021 and September 2023 and analysed using ELISA method. Bovine emerged as the most frequent blood meal source, followed by humans and chickens (Bursali et al., 2024b). These mosquitoes exhibited a zoophilic tendency feed on available hosts in the vicinity, with domestic animals. The proportion of blood meals from different hosts generally reflected their relative abundance in the villages (Bursali & Şimşek, 2022; Bursali et al., 2024c). Similarly, *An. sacharovi*, known for its primarily zoophagic (animal-feeding) behaviour, has been the subject of feeding pattern studies worldwide. These mosquitoes predominantly feed on animals, with cows as the preferred host in Senegal (Gueye et al., 2023; Ngom et al., 2013). Human blood meals were rare (<7%), contrasting with reports of higher human feeding rates in Iran. Additionally, some mosquitoes exhibited mixed blood meals, suggesting feeding on multiple hosts. Asale et al. (2017) suggested that control measures might be driving this low human feeding rate, forcing mosquitoes towards alternative hosts like livestock. Notably, despite the abundance of birds, no avian blood meals were detected, aligning with past observations. The proximity of certain animals, such as cattle, to human habitation may significantly influence the host-seeking behaviour of certain vectors. For instance, a positive association was found between the presence of cattle and the abundance of *Anopheles pharoensis*, a known malaria vector in Ethiopia (Zeru et al., 2020). This potentially translates to an increased risk of malaria transmission in such settings. Conversely, other mosquito species, including *An. gambiae* (s.l.) and *An.tenebrosus*, may not exhibit such a response to the presence of cattle. Therefore, implementing strategies that maintain a physical distance between cattle enclosures and human dwellings could be a valuable approach for mitigating malaria transmission (Zeru et al., 2020). *Culex* mosquitoes exhibit even greater variation in host selection, as reported in studies across diverse locations (Gomes et al., 2001; Guta et al., 2021). Their targets can range primarily from birds to humans. Bursali and Şimşek (2022) found that the majority of *Cx. pipiens* (86.5%) and *Cx. tritaeniorhynchus* (97.14%) in their field study fed on cows. Conversely, *Cx. quinquefasciatus* in Kenya showed a higher tendency to feed on humans indoors (Muturi et al., 2008). A study (Börstler et al., 2016) in Germany analysed the blood meals of mosquitoes collected between 2012 and 2015 using various traps and techniques. They identified 32 different host species for 23 mosquito species, including *Ae. vexans*, *Cx. pipiens pipiens* and *Ochlerotatus cantans*, with most mosquito meals coming from non-human mammals (74%), followed by humans (20%) and birds (7%). The most common blood sources were deer, humans, cattle and wild boar. Interestingly, there was not a significant difference in feeding patterns based on location or time of year for the three most common mosquito species. While investigating mosquito blood-feeding patterns in southeast England, Brugman et al. (2017) collected a substantial sample (20,666) of mosquitoes from a wetland habitat known for its resident and migratory birds. Over 10% (2159) of the collected mosquitoes had fed on blood, and subsequent analysis of a subset (1341) successfully identified the vertebrate source of the blood meal in over 70% (964) of the cases. The most prevalent blood-fed mosquito species belonged to the *An. maculipennis* complex (73.5%), followed by *Culiseta annulata* (21.2%) and *Cx. pipiens* form *pipiens* (10.4%). Notably, the study documented blood feeding on a diverse range of vertebrate hosts (19 species), including both mammals (5 species) and birds (14 species), with migratory bird species represented among the avian hosts. Furthermore, the study revealed bird feeding behaviour by *Cx. modestus* and *An. atroparvus*, which are mosquito populations not previously known to target birds in England. Bouafou et al. (2024) employed field-based methods and statistical models to investigate how habitat type and seasonal variations influence the host-seeking behaviour of various *Anopheles* mosquito populations in LaLopé National Park, Gabon, Central Africa. Notably, the study documented the consistent presence of major malaria vectors (*Anopheles coluzzii*, *An. gambiae* and *An.unestus*) even in areas with minimal human activity. The findings revealed a significant influence of human presence on both the biodiversity and abundance of *Anopheles* mosquitoes, confirming the presence of these key vectors within the park's protected areas. Interestingly, although host feeding preferences remained consistent across habitat types, a general increase in human-seeking behaviour was observed for all mosquito species within the park's natural settings. This finding suggests that malaria vectors may be adapting to exploit humans even in protected areas (Bouafou et al., 2024).

Expanding upon the known host range of mosquitoes, several studies (Cupp et al., 2004; Miyake et al., 2019; Tamashiro et al., 2011) documented blood feeding behaviour in mosquito species such as *Culex peccator*, *Culex erraticus*, *Ae. albopictus* and *Uranotaenia* spp. on non-terrestrial vertebrates. These observations included air-breathing fish (mud lobster *Thalassina anomala*), amphibians (*Rana* spp.) and land crabs (*Cardisoma carnifex*, *Discoplax*).

Sandflies exhibit a remarkable diversity in their feeding preferences, as evidenced by several studies (Azmi et al., 2020; Elaagip et al. 2020; Jibreel et al., 2023; Maia et al., 2013; Palit et al., 2005). This variation is observed not only between species but also within populations of the same species. Although some sandflies primarily feed on animals (zoophilic), others are opportunistic and target a wider range of hosts, including humans. Palit et al. (2005) investigated the feeding behaviour of *Ph. argentipes* and *Ph. papatasi* in West Bengal, India, a region endemic for Kala-azar (VL). They revealed that a significant difference in host preference between the two species. *Ph. argentipes* were primarily zoophilic (feeding on animals) with a preference for humans as the secondary choice (62.80% and 24.92%, respectively). These species exhibited an opportunistic behaviour but there was a higher prevalence of multiple blood meals in *P. argentipes*. Similarly, a study (Maia et al., 2013) conducted in the Algarve region of southern Portugal observed that *Ph. perniciosus* exhibited an opportunistic feeding behaviour with no clear host preference. Females were found to have fed on a variety of hosts, including chickens, rodents and cats. This finding aligns partially with prior research from Spain (De Colmenares et al., 1995) and Italy (Bongiorno et al., 2003), which also reported opportunistic feeding tendencies in *Ph. perniciosus*. Field-based research by Garlapati et al. (2012) and Yared et al. (2019) identified a significant proportion of sandflies harbouring blood from multiple vertebrate hosts. Azmi et al. (2020) investigated blood meal origins in sandflies collected from Palestinian regions. They identified 20 species, with *Ph. papatasi* and *Ph. sergenti* being the most abundant. Analysis revealed these species fed on a variety of hosts, including humans, hyraxes, rats, livestock (cows and goats) and birds. Notably, 7.7% of *Ph. sergenti* females contained mixed blood meals with both hyrax and rat DNA. This suggests hyraxes could be potential *Leishmania tropica* reservoirs in the study area. Another study (Jaouadi et al., 2018) in Tunisia between 2015 and 2016 captured 690 sandflies belonging to *Phlebotomus* and *Sergentomyia* genera. Blood meal analysis revealed a dominance of human blood (42.85%), followed by rodents (*Mus musculus* and *Rattus norvegicus*) and livestock (cattle, rabbits, sheep and goats). These studies demonstrate the broad host range of sandflies, with humans being a significant blood source in some areas. The presence of blood from animals (e.g. hyraxes in palestine) that could potentially harbour *Leishmania* parasites strengthens the concern for disease transmission. In another study in the Bethlehem District of Palestine, Salah et al. (2020) revealed that *Ph. sergenti*, a sand fly species fed on a diverse range of hosts. Their blood meal analysis identified four hosts: human (45.5%), livestock (25%), avian (19.9%) and dog (9.6%). González et al. (2015) collected 26 blood-fed sandflies from three locations: Fuenlabrada (Madrid), Girona (Catalonia) and Minorca (Balearic Islands) in Spain. Although *Ph. perniciosus* was the dominant sand fly species, their bloodmeal preferences varied depending on the location. Wild animals, particularly rabbits and hares, were the primary blood source. Human blood meals were limited, but mixed feeding with sheep, goats and humans was observed in some cases (from Girona and Minorca). Srinivasan et al. (2015) collected 19 sand fly species, with *Sergentomyia baghdadis* being the most abundant, followed by *Ph. argentipes* in the Kani tribe settlements of Kerala, India, an area known for cases of CL. Sandflies were significantly more abundant indoors than outdoors. *P. argentipes* was particularly concentrated in cattle sheds compared to human dwellings and outdoors. The sampled flies fed on multiple hosts. They also found that during summer, the sandflies preferred the upper portions of walls and ceilings inside houses, during monsoon season, they were found lower on walls and in cooler months, they did not show a height preference. The proportion of sandflies in different stages of feeding (full-fed, half-gravid and gravid) did not vary significantly indoors, suggesting they remained inside after feeding. Chaskopoulou et al. (2016) identified *Phlebotomus perfiliewi*, *Phlebotomus simici*, *Phlebotomus tobbi*, *P. Papatasi*, *S. minuta* and *Sergentomyia dentata* in Thessaloniki, Greece. They observed that sandfly activity peaked in mid-August to mid-September then declined sharply in October. *Ph. perfiliewi* (the most prevalent) and *Ph. simici* primarily fed on humans (88% and 95%, respectively). These two species also fed on chickens and goats. This study highlights the importance of focusing control efforts during peak activity months (August–September) and targeting areas with animal facilities near human settlements. Yared et al. (2019) investigated sand fly blood meal sources in Kafta Humera, Ethiopia, an area endemic for VL. They found that over three-fourths (74.93%) of the sandflies collected were *Ph.orientalis*, whereas the remaining belonged to nine other species such as *Sergentomyia clydei*, *P. papatasi*, *Sergentomyia schwetzi*, *Phlebotomus bergeroti* and *Sergentomyia africana*. The most common blood meal source for the sandflies was donkey (33.9%), this was followed by cow (24.2%), human (17.6%), dog (11.8%) and goat or sheep (8.6%). Mixed blood meals from different sources were found in 28.2% of the sandflies and unidentified blood meals, likely from wildlife, were found in 15.28%. No Leishmania parasites were detected in any of the sandflies tested, which is consistent with the expected low infection rate (1–5 out of 1000). A study in Sicily (Abbate et al., 2020) found *S. minuta* and *P. perniciosus* were much more common than other species like *Ph. sergenti*, *Ph. perfiliewi* and *Ph.neglectus*, which were rarely seen. The two dominant species had different preferences for feeding with *Ph. perniciosus* mostly determined to have fed on wild rabbits, whereas *S. minuta* primarily targeted humans for blood meals (about two-thirds of the time). The study also identified other animals like horses, goats, pigs, dogs, chickens, cows, cats and donkeys as blood sources for these sandflies. Elaagip et al. (2020) revealed human DNA in 6.4% of females during blood meal analysis of *P. orientalis* using multiplex PCR assay in Sudan, indicating some anthropophilic feeding behaviour. In eastern Sudan, Jibreel et al. (2023) reported that *P. orientalis* had a preference for cows and donkeys. In another study (Yuko et al., 2022), field-collected sandflies species, including *S. schwetzi*, *S. clydei*, *Sergentomyia antennata*, *Sergentomyia squamipleuris*, *S. africana* and *P. martini* from a Ntepes virus area in Kenya, were found to primarily feed on humans, suggesting a high potential for human exposure to this pathogen, the sandflies were not tested for NTPV transmission. Karagul and Kasap (2024) analysed over 200 sand fly specimens and identified nine different vertebrate hosts, including cows (*Bos taurus*) as the most common, followed by chickens (*Gallus gallus*) and goats (*Capra hircus*) in Türkiye. Interestingly, most of the sand fly species primarily feed on bovines. Humans were only a minor blood source for these sandflies. Among the examined species, *Paraphlebotomus* sandflies stood out with a broader host range, particularly favouring birds.

Sciopemyia aff. microps, *Sciopemyia sordellii* and *Martinsmyia oliveirai* collected from inside ferruginous caves in Serra do Gandarela National Park and Serra do Rola Moça State Park, Brazil were determined to feed on cold-blooded animals in natural habitats. Frogs of the family Hylidae were the main hosts (Costa et al., 2021). Analysis of the blood feeding patterns of three sand fly species (*L. longipalpis, Migonemyia migonei* and *Lutzomyia lenti*) captured in Brazil revealed a diverse range of vertebrate hosts. Humans were the most frequent blood source (73%), followed by chickens (23%), dogs (22%), horses (15%), black rats (11%) and cats (2%). Notably, a high proportion (76.1%) of *L. longipalpis* females specifically fed on human blood. Interestingly, the study also documented multiple feeding behaviour, with 48% of the tested females having fed on a single source, 31% on two sources and 12% on three distinct vertebrate hosts (Silva Sales et al., 2015). Chaves and Añez (2004) explored the structure of the sand fly community in the Venezuelan Andes to elucidate its potential role in the transmission of American cutaneous leishmaniasis. Null-model tests were employed to analyse the distribution patterns of sand fly species across various living zones (habitats) and altitudinal gradients. The analyses revealed a lack of aggregation among sand fly species at both spatial scales, indicating no preferential co-occurrence in specific habitats or altitudes. Additionally, the results suggested a high degree of similarity in resource utilization strategies across different sand fly species. This observation, coupled with the absence of spatial aggregation, implies the potential for these sandflies to constitute a unique functional group, or guild, within the Andean ecosystem. Furthermore, the co-occurrence of anthropophilic and zoophilic species, presumably exploiting the same blood resource, strengthens the hypothesis of a unified sand fly guild (Chaves & Añez, 2004). Anaguano et al. (2015) reported that the majority (77%) of blood meals of *Lutzomyia* sandflies in Ecuador originated from avian (bird) sources *with Nyssomyia trapidoi* identified as the most prevalent species feeding on birds. Mammalian blood meals were less frequent (16%). A small percentage (7%) of sandflies had mixed blood meals (both avian and mammalian). Species-Level analysis revealed that chicken blood was the most detected avian source (35.5%). Human (2.8%), cow (2.8%) and dog (1.9%) blood were also identified among the mammalian meals. Similarly, 10 different vertebrate species have been identified to be the blood source of these meals of 141 blood-engorged female sandflies. Five species (*Lutzomyia evansi*, *Lutzomyia panamensis*, *Lutzomyia micropyga*, *Lutzomyia shannoni* and *Lutzomyia atroclavata*) fed on humans. This is the first evidence of anthropophily for *L. micropyga* and *L. atroclavata* in this region. Cattle, donkeys, humans and pigs were identified as frequent blood meal sources compared to other animals Mabuya lizard (*Mabuya* sp.), Anolis lizard (*Anolis* sp.) and wild boar (*Sus scrofa*) analysed (Paternina et al., 2016). Over 13 months, Ávila et al. (2018) collected over 2500 sandflies belonging to 43 species. They revealed higher sand fly diversity in rural areas compared to urban environment with three species, *Trichophoromyia auraensis*, *Trichophoromyia* spp. and *Evandromyia saulensis*, being particularly abundant, and analysis of blood meals from fed sandflies indicated that all samples originated from domestic chickens. A variety of blood sources, including humans, chickens, dogs, ducks and pigs, were found in the abdomen of *Pintomyia evansi*, *Micropygomyia cayennensis*, *Lutzomyia gomez*, *Psychodopygus panamensis*, *Pintomyia rangeliana* and *Micropygomyia trinidadensis* collected from villages in northern Colombia. The most common blood source these sandflies was human (72%), followed by chicken (12%) and dog (8%) and most of the tested flies were positive with *L. infantum* and *L. panamensis* (González et al., 2018). Similarly, blood meal analysis of 12 engorged female sandflies belonging to three genera: *Brumptomyia* spp., *Evandromyia* spp. and *Nyssomyia* spp. in Peridomiciles, Brazil, revealed that the sandflies had fed on blood from a variety of vertebrate hosts, including both wild and domestic animals, as well as humans mostly from wild boar (*S. scrofa*) (50%) followed by humans (16.67%) (Leonel et al., 2024). Identifying the predominant sand fly species and their host preferences in a specific region is crucial for targeted control measures. These findings also help in understanding Leishmaniasis epidemiology. Predominantly zoophilic species (*Ph. papatasi*, *Ph. major* s.l., *Ph. neglectus*, *Ph. kandelakii* s.l., *Ph. perfiliewi* s.l. etc.) feed on animals like dogs, cows and pigs, whereas anthropophilic species (*P. sergenti*) target humans. The presence of multiple blood meals within individual sand fly species (*P. perniciosus*, *P. argentipes* and *Phlebotomus mascittii*) that exhibit opportunistic feeding depending on host availability (Garlapati et al., 2012; Yared et al., 2019) further emphasizes their broad host range. Host body size may be a factor, with larger animals offering a larger target area and potentially emitting more attractive odours and heat (Azizi et al., 2008; Yared et al., 2019). Sandflies exhibit multiple blood feeding within a single host. This is less common in mosquitoes.

Numerous other studies have shown that sandflies exhibit diverse feeding behaviours across the globe (Cera-Vallejo et al., 2024; Macedo-Silva et al., 2014; Paternina et al., 2016; Sant'Anna et al., 2008; Sales et al., 2015; Tiwananthagorn et al., 2012). There can be variations across both Old World and New World species as different sandfly genera have evolved adaptations to specific environments (Akhoundi et al., 2016). For example, *Phlebotomus* species are more common in drier, semi-arid areas spanning the Mediterranean, Afrotropical regions, Middle East and Asia. They tend to feed on animals like dogs and cows. *Sergentomyia* dominates in tropical regions are in Afrotropical, Oriental and Australasian regions where *Phlebotomus* is scarce and may target humans more frequently. New World Sand Flies in the genera *Lutzomyia*, *Warileya* and *Brumptomyia* thrive in tropical forests in the Nearctic (southern North America) and Neotropical (Central and South America) regions (Akhoundi et al., 2016). The types of hosts available in these preferred habitats will influence their feeding patterns. In a forest, sandflies might primarily feed on forest-dwelling mammals and birds, whereas in a savannah, they might target larger herbivores. The distribution patterns of potential blood sources within a habitat can also play a role. Sandflies are more likely to feed on hosts that are readily available and accessible within their preferred microhabitat. This can lead to variations in feeding behaviour even within the same sand fly species across different locations. New World sandflies, particularly those in the genus *Lutzomyia*, exhibit a much wider range of vertebrate hosts including humans, livestock wild mammals (rodents and marsupials), birds and even reptiles, compared to their Old-World counterparts, and tend to feed in an opportunistic way (Roque & Jansen, 2014; Rohousova et al., 2015). Even though not all sandflies that feed on potential *Leishmania* reservoirs become infected or transmit the disease, a wider host range can complicate Leishmaniasis transmission because identifying animal reservoirs becomes more challenging. Moreover, some animals like cats are often considered asymptomatic hosts of the parasite without serving as a reservoir (Aksulu et al., 2021).

The blood-feeding behaviour of these hematophagous insects is not constant through time and space. Many species exhibit a degree of phenotypic plasticity, meaning they can adjust their behaviour based on environmental factors and available resources (Lefèvre et al., 2009; Orsborne et al., 2018). Factors influencing blood-feeding behaviour include host availability where these insects will feed on the most readily available blood source in their environment. This can lead to a shift in feeding preference depending on the abundance of different host species (e.g. humans, livestock and birds) in a particular location and also feeding success from available host availability can be impacted by factors such as host defences (Azizi et al., 2016; Fikrig et al., 2022; Gebresilassie et al., 2015). Another important factor are environmental conditions like temperature, humidity, and light that can influence activity levels and blood-feeding patterns (Balenghien et al., 2006). Widespread insecticide use can lead to changes in mosquito and sandfly behaviour as they try to avoid treated areas. This might cause them to shift feeding times or seek refuge outdoors, altering their contact with potential hosts (Ferreira et al., 2017). Based on data collected from studies, even when certain species typically prefer human blood in lab settings, field studies often show a broader host range (cows and birds) depending on their local environment. These vectors can adjust their feeding time based on light availability (becoming more active at dusk or dawn) to avoid predators or maximize contact with potential hosts. This ability to adjust behaviour allows them to adapt to changing environments and maximize their survival and reproductive success. However, from a disease control perspective, it can make it challenging to predict their behaviour and develop targeted interventions. There can be discrepancies between controlled laboratory settings and field data (Ramesh et al., 2015; Tuno et al., 2017), highlighting the need for a combined approach for a comprehensive understanding of feeding behaviour.

8 | IMPACT OF HOST DEFENSIVE BEHAVIOUR ON BLOOD FEEDING

Animals defend against insect bites using physical barriers like skin and feathers, as well as behavioural adaptations such as physical movements and avoidance strategies (Mooring et al., 2007; Terrill & Shultz, 2023). Defence movements such as tail flicking, hear and head shaking, skin shaking and leg shaking are common defensive behaviour employed by livestock and wild animals and a strong correlation can be found between fly density and the frequency of these movements (Desquesnes et al., 2022; Matherne et al., 2018). Additionally, human ingenuity has contributed to the development of artificial defensive measures such as sticky traps, house screening and insecticide-treated bed nets, all of which have proven highly effective in reducing mosquito and sandfly feeding success (Takken, 2002; Lindsey et al., 2002; Bursalı, 2013). These defensive behaviours can significantly hinder insect feeding by physically obstructing their attempts to feed or by causing them to abandon the feeding process altogether (Lyimo & Ferguson, 2009). The widespread use of bed nets and indoor residual spraying (IRS) has indeed placed significant selective pressure on mosquito populations, leading to documented changes in their biting and resting behaviour such as a potential shift in of insect feeding behaviour towards outdoor feeding and seeking refuge outdoors. This could be due to insects avoiding areas treated with insecticides used in bed nets and IRS. Although some species naturally feed outdoors, this shift can increase the risk of disease transmission in areas where outdoor control measures are less prevalent. To avoid contact with insecticides, some vectors might adjust their feeding times to bite earlier or later in the evening when people are less likely to be under bed nets (Ferreira et al., 2017; Kreppel et al., 2020; Takken et al., 2024). Due to less research focus on sandflies compared to mosquitoes, the long-term effects of control methods on sandfly populations and behaviour are not fully understood.

9 | CONCLUSION

Vector-borne diseases, transmitted by sandflies and mosquitoes, pose a significant threat to global health. While enjoying a meal, these insects inadvertently act as disease vectors. Pathogens present in their saliva or ingested blood can be transmitted to the host, causing illnesses like malaria, leishmania, dengue fever and Zika virus. This blood-borne transmission causes immense human and animal suffering and economic hardship, particularly in developing countries. The relationship is built on adaptations from both sides. These insects boast sophisticated sensory systems (smell and sight) to locate hosts, whereas some have developed preferences for specific types (humans and animals). Meanwhile, some hosts possess defences like thicker skin or immune responses to deter feeding. Delving deeper into this intricate relationship between mosquitoes and sandflies, their hosts and blood feeding is crucial. Even though mosquitoes and sandflies were chosen as the primary focus of this study, it is essential to acknowledge that other important vectors, such as ticks, triatomine bugs and midges, also play critical roles in transmitting a variety of pathogens. Given the breadth of the topic, these vectors were not dealt with. The exclusion of these vectors limits the comprehensive understanding of vector-borne disease transmission. By understanding their behaviour, adaptations and disease transmission mechanisms, we can develop more effective control strategies and protect ourselves from vector-borne threats.

AUTHOR CONTRIBUTIONS

Fatma Bursali and Mustapha Touray: Conceptualization; investigation; writing – original draft; writing – review and editing; data curation.

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