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ARTHROPODS AND MEDICAL ENTOMOLOGY - REVIEW

Blood feeding habits of mosquitoes: hardly a bite in South America

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Abstract

Mosquito blood feeding plays a key role in epidemiology. Despite its importance and large number of studies worldwide, less attention has been paid in South America. We summarized some general concepts and methodological issues related to the study of mosquito blood feeding habits, and compiled and analyzed all published information regarding the subject in the continent until 2020. Available literature comprised 152 scientific studies, that pursued different approaches: human landing catches (102 studies), baited trap (19), and blood meal analyses of collected specimens (38). Among the latter, 23 used serological and 15 molecular techniques. Species most frequently studied were those incriminated in malaria transmission, whereas relevant vectors such as *Aedes aegypti*, *Ae. albopictus*, and *Haemagogus janthinomys* were surprisingly neglected. Brazil was the leading country both in number of works and species studied. For over 70% of the species and three out of 13 South American countries there is no single information on mosquito blood feeding habits. Data from baited traps included 143 mosquito species, 83.9% of which were attracted to humans, either exclusively (10.5%) or in combination with other vertebrates (73.4%). Host blood identification of field collected specimens provided data on 102 mosquito species, and 60.8% of these fed on humans (55.9% combined with other vertebrates). Only 17 of the 73 species assessed by both methods yielded similar feeding patterns. Finally, supplementary tables are provided in a comprehensive summary of all information available and information gaps are highlighted for future research in the continent.

Keywords Baited traps · Blood meal analysis · Host feeding patterns · Host preference · Human landing · Mosquito-borne diseases

Introduction

Approximately 60% of human emerging infectious diseases, and many recent pandemic threats, such as H1N1, Ebola, and SARS-CoV-2, have a zoonotic origin, i.e., they were transmitted from animals (Cross et al. 2019). Mosquitoes (Diptera: Culicidae) are among the most important vectors of pathogens for vertebrates, carrying diverse etiological agents such as viruses (e.g., yellow fever), protozoa (e.g., *Plasmodium*), and filariae (e.g., *Wuchereria*) (Service 1993). As, in any case, the completion of a transmission cycle requires the coexistence in space and time of the host (or reservoir), the vector and the pathogen, the interaction between the first two is essential for the acquisition of the pathogen by the vector and its subsequent transmission to another host (Molaei et al. 2008). This occurs during blood ingestion, in which the mosquito can acquire a pathogen together with blood from an infected host. Viruses and protozoa begin to reproduce within the mosquito digestive tract, and after a lapse of time called extrinsic incubation period, migrate to the salivary glands (Ohm et al. 2018). Thus, the mosquito becomes capable of transmitting the pathogen to a susceptible host in a subsequent bite while it injects anticoagulants and anesthetics (Nouzova et al. 2019). Regarding filariae, small larvae

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ingested together with the blood develop from microfilaria (L1) to infective mature form (L3) in different parts of the insect body depending on the species and then migrate to the mouthparts of the vector. The infection occurs when the mosquito takes a new blood meal and L3 are deposited on the skin and actively penetrate the host through the wound of the mosquito bite (Anderson 2000). Independently of the pathogen, mosquitoes may infect more than one vertebrate host species, but only some of them develop high enough pathogen loads to infect the vectors that feed on them (Kuno and Chang 2005). The remainder infected species, termed dead-end hosts, are irrelevant in terms of disease propagation but may anyhow be of great concern if they are humans, domestic animals, or protected wildlife.

In this context, mosquito blood feeding habits play a key role in diseases transmission cycles to evaluate how vector populations determine the intensity of transmission (Molaei et al. 2008). Understanding blood feeding habits can also improve disease management strategies, such as targeted vector control to reduce vector-host contact, and contribute to forecasting future disease risk in human and other animal populations (Lyimo and Ferguson 2009). These are the reasons why, since the beginning of the twentieth century, researchers have attempted to characterize host preference and identify mosquito blood meals by different techniques, and the results of these investigations have been embodied in several revisions. Tempelis (1975) proposed nine basic feeding patterns and compiled blood meal analysis techniques by serology, and 8 years later Washino and Tempelis (1983) summarized the status of host blood meal identification studies, including both serological and non serological approaches, and updated the work published since 1975. Over two decades passed until Lyimo and Ferguson (2009) reviewed the ecological and evolutionary determinants of host choice in mosquitoes and other vectors of human disease. Then, a comprehensive work by Takken and Verhulst (2013) was focused on the available knowledge on feeding habits worldwide, focusing on the intrinsic and extrinsic factors that modulate them. Other recent reviews targeted particular geographical areas or species, e.g., Stephenson et al. (2019) compiled mosquito feeding studies in Australia and Cebrián-Camisón et al. (2020) dealt with invasive *Aedes* species in Europe. Although prolific work has been performed on evolutionary aspects of blood feeding habits and species-specific studies in other continents, relatively little is still known about what mosquitoes feed on in South America.

The aim of this work is (a) to summarize some general concepts and methodological issues related to the study of mosquito blood feeding habits, (b) to review the available information for South America, and (c) to identify gaps or vacancy areas to outline future research interests.

General concepts

Set the table: what do mosquitoes eat?

Mosquitoes of both sexes drink water and feed on plant sugars including floral nectar, fruit juices, exudates from damaged plant tissue, and plant-derived sugars from insects such as honeydew (Clements 1992; Peach et al. 2019). Males are strictly phytophagous and require frequent intakes for survival, and if deprived of sugar, they typically die within four days after hatching (Gouagna et al. 2014). Also, their swarming ability and insemination rates depend on nectar availability (Gary et al. 2009). Females mating with sugar-fed males have been reported to present increased ovarian lipid content, less follicle reabsorption, and more longevity (Baldini et al. 2012; Clifton et al. 2014; Barredo and DeGennaro 2020). Plant sugars also serve as source of energy for female mosquitoes during the first days after emergence, a period in which the female's primary ovarian follicles develop to the pre-vitellogenic resting stage and the ability to find hosts is generated (Clements 1999; Lourenço de Oliveira 2015).

Hematophagy is characteristic of female mosquitoes of most genera, as blood obtained from hosts is a source of metabolic energy and its proteins are essential for egg production (Clements 1992). There are some exceptions, such as all species of *Toxorhynchites* and *Malaya*, and possibly some species of *Topomyia*, *Maorigoeldia* and other genera which feed exclusively on plant-derived sugars, a trait know as autogeny type II (Service 1993; Reeves et al. 2018a). Alternatively in autogeny type I, which is present in some species (e.g., *Ae. taeniorhynchus*, *Cx. pipiens molestus*), females produce eggs without blood feeding for their first oviposition but must imbibe blood for subsequent ones, and this can be obligate or facultative; in the latter case depending upon environmental conditions (O'meara and Evans 1977; Reeves et al. 2018a).

During a gonotrophic cycle, female mosquitoes ingest and digest a blood meal, retrieve nutrients and excrete waste products to produce viable eggs. At each bite, a hematophagous female imbibes approximately 30 µL of blood of which around 10% of the protein amino acid carbon goes to the eggs (≈ 4% as proteins and 6% as lipids), 20% is retained in the female (10% proteins, 8% lipids, 2% sugars), and the majority is oxidized and excreted as waste (Scaraffia 2016). Female mosquitoes feed on all vertebrate lineages, i.e., mammals, birds, reptiles, amphibians, and fish (Tempelis 1975; Tamashiro et al. 2011; Takken and Verhulst 2013; Miyake et al. 2019). Recent findings indicate that some mosquito species also feed on invertebrates, as is the case of *Uranotaenia sapphirina* feeding on annelids (Reeves et al. 2018a).

Host feeding and host preference patterns

Let us begin by defining two important concepts. The host feeding pattern of a mosquito population is the distribution of feeds taken on different hosts at a specified time and place. It can be influenced by a large number of intrinsic and extrinsic factors to the mosquito species, as will be detailed later in this section. For its part, host preference refers specifically to the tendency to feed on a particular host (or group of hosts) in greater proportion to its abundance in the environment. It is a solely intrinsic trait, determined genetically (Fikrig and Harrington 2021). Throughout this work, both concepts are referred together by using the general expression "blood feeding habits". Although plant feeding is also an important aspect of mosquito biology, for the purpose of this review, "hosts" are restricted to blood sources.

Female mosquitoes use a range of senses to accurately identify hosts in a heterogeneous environment, from which olfaction is considered more important than vision and taste (Takken and Verhulst 2013). Host substances to which mosquitoes give a positive response are known as kairomones, i.e., chemical compounds that evoke a behavioral or physiological response that is adaptively favorable to the receiver but not to the emitter. Some of these compounds are volatile and serve as host cues, for example breath, epidermal secretions and their bacterial decomposition products, flatus, and urinary and fecal contaminants of the body surface (Clements 1999).

Some mosquito species are generalists and express opportunistic feeding behavior, whereas others are specialists and feed preferentially on selected hosts. In this regard, substantial research has been performed to try to predict how organisms should select feeding resources to maximize their fitness. If the frequency of encounters with favorable host species is high and net energy is gained when only a limited subset is consumed, host specialization is predicted (Lyimo and Ferguson 2009). In environments with low chance of host encounter, waiting for an optimal host is traded-off against the risk of dying before feeding on a suboptimal host. In this case, moderate differences in energetic gains favor generalism (Egas et al. 2004; Lyimo and Ferguson 2009). Evidently, mosquito species with little host preference will be less affected by the distribution of a particular host than species with a narrow host range (Burkett-Cadena et al. 2014).

Variability in blood feeding habits is observed among species, among populations of the same species and even within a population. These differences are caused by intrinsic and extrinsic factors and can vary spatially and temporally. The former include innate tendencies or genetics (individuals are more likely to feed on the same host as previous generations), issues related to flight, the nutritional state of the mosquito (nutrition-poor individuals are more likely to feed on non-preferred hosts), and behavioral characteristics (e.g., tendency to feed indoors/outdoors, feeding time and frequency) (Ulloa et al. 2004; Lyimo and Ferguson 2009; Takken and Verhulst 2013). Extrinsic factors are those dependent on the hosts (availability, abundance, defensive behaviors, chemicals released), climatic variables and habitat characteristics (Clements 1999; Takken and Verhulst 2013; Stephenson et al. 2019).

Plasticity in host preference has been observed in many mosquito species, for instance when the favorite host species are unavailable and the response threshold for host selection has been lowered due to low energy reserve, or when adverse climate prevents mosquitoes from moving away from their habitat (reviewed by Takken and Verhulst 2013). Many *Culex* species are reported to feed preferably on birds during spring and summer, but when bird abundance decreases they switch to other hosts including humans (Kilpatrick et al. 2006; Simpson et al. 2012). This suggests that, although inherent preferences may prevail locally, some species are adapted to obtain blood in many different circumstances where the most abundant host species appears to be selected. At its most extreme, host availability can impact mosquito feeding behavior by influencing whether they blood feed at all. Autogenous egg production has been associated to species living in environments in which host availability is severely limited (Corbet 1967; Lyimo and Ferguson 2009).

Blood feeding habits greatly impact pathogen acquisition and transmission. A generalist species is less likely to transmit a single host pathogens than a specialist feeder, given that the probability of biting the same host twice consecutively is low. On the other hand, generalist feeders are more prone to act as bridge vectors for zoonotic infections by transmitting a pathogen from a reservoir host to other susceptible hosts (Fikrig and Harrington 2021). Besides affecting the dispersal capacity of the pathogen, the type of host selected can also condition egg production and, therefore, affect vector abundance (Takken and Verhulst 2013). As hosts differ considerably in their ability to become infected and transmit pathogens to vectors, an environment with a greater diversity of hosts can promote a dilution effect. This means that low competent hosts reduce the probability of infection of highly competent hosts, resulting in less human risk (Schmidt and Ostfeld 2001).

Approaches for the study of mosquito blood feeding habits

Studies on feeding habits are usually performed by examining the blood meal of specimens collected by different techniques in the field or by registering mosquito preference in situations of host choice. Therefore, the results of a given study and the conclusions derived from it depend on two major issues, namely the method used to collect mosquitoes and, if applicable, the blood meal analysis technique.

Collection methods

There is a wide variety of methods for collecting hematophagous mosquitoes, compiled by Silver (2008). These can be classified in methods focused on studying active mosquitoes (whether using or not attractants) and those intending to collect the resting mosquito population. Attractant techniques involve traps with light and/or CO_2, visual attraction traps and sounds, and also animal or human bait catches, all of which collect mainly host-seeking females. Non-attractant methods target the general active mosquito population including females without host-seeking behavior and include stationary nets, Malaise traps, sticky traps and vehicle-mounted traps, among others. Devices for collecting resting specimens from natural environments or indoors include oral or battery-powered aspirators (e.g., backpack), hand-nets, and resting boxes. The different types of traps and devices can be combined depending on the specific aim of the study, e.g., human landing catches using oral aspirators adding CO_2 as attractant to characterize anthropophilic species.

Attractant methods collect mostly unfed females searching for a blood meal and the choice of bait or attractant will determine the group of mosquitoes captured, e.g., mammophilic or ornithophilic species. Although these techniques preclude collecting engorged females for blood identification, they are valuable in controlled experiments of host selection. Particularly, human bait or landing catches have been used for many years and remain the most useful method to collect anthropophagic species. Variations on the simple direct bait catch have included enclosing humans (or other animals used as bait) in nets, cages or traps. Human landing catches are easily performed and require no complicated or expensive equipment, but are time and personnel consuming, subject to interoperator and location variability, and impractical in many urban environments (Silver 2008). They can also present ethical issues if the study region is under transmission of mosquito-borne diseases (Achee et al. 2015), which can be solved with the human-baited double net trap proposed by Tangena et al. (2015).

Other attractant devices like CDC-light traps, mosquito oviposition traps (MOT) and BG-sentinel traps, are more effective at capturing large numbers of mosquitoes, but are biased toward collecting individuals of certain species at different developmental stages (e.g., MOT are mainly used to collect eggs and females of *Ae. albopictus*) and physiological states (Silver 2008; Li et al. 2016). Furthermore, the high cost and the dependence on personnel for setup and recovery preclude their use in large-scale collections, particularly in resource-poor settings (Vazquez-Prokopec et al. 2009).

Collections obtained with non-attractant traps are less biased and should be representative of all species present. However, they only sample the proportion of the population that is active, comprising unfed females (although they may not all be actively host seeking) and active males. A disadvantage of non-attractant traps is that the numbers obtained are small unless mosquito populations are large because they catch mosquitoes only in their immediate area. Although efforts are made to minimize sampling bias, the sole physical presence of a trap may promote visual responses, causing mosquitoes to be either attracted or repelled by it (Silver 2008).

Adult mosquitoes, which spend most of their time resting, are not properly sampled with attractant and non-attractant traps. Resting collections include blood fed females and can be particularly useful to identify blood meals in the field. Although the search for outdoor resting mosquitoes (e.g., amongst vegetation, in hollow trees, animal burrows) can be time-consuming and unrewarding, worthwhile numbers of mosquitoes have been obtained by aspirating, sweep-netting or the use of artificial resting shelters (Chandler et al. 1976a, 1976b; Nasci and Edman 1984; Komar et al. 1995). In the case of indoor collections, battery-powered aspirators, like the CDC-backpack aspirator, are considered the most effective method for catching certain domestic mosquito species (Edman et al. 1992; Clark et al. 1994). Vazquez-Prokopec et al. (2009) designed a mosquito aspirator with the same aspiration capacity of the CDC Backpack Aspirator, but with several advantages as smaller, lighter and cheaper.

In brief, animal baited traps can be useful to answer which mosquito species feed on certain animals, and to study preference among a set of hosts offered in an artificial or semi field setting. To obtain engorged females in the field, techniques focused on collecting the resting mosquito population are most appropriate. This approach, although time and space dependent, can aid in the understanding of biting risk and, as evidence accumulates, whether it provides robust results on host feeding patterns it can suggest host preferences (Fikrig and Harrington 2021).

Alternatively to assess preference in natural conditions, hosts availability in the environment should be surveyed. This can be accomplished by various methods: transect surveys, animal trapping/trampling, camera traps, household interviews, and previous published or unpublished data on the study area. This information is then coupled with blood meal identifications in the calculation of feeding metrics which indicate host preference or avoidance. Hess et al. (1968) introduced the forage ratio into mosquito studies, first proposed by Savage (1931) for herrings. This index compares the relative propensity for blood feeding on all hosts in the population by dividing the proportion of all blood meals that were taken from a given animal by the proportion that animal comprises of the total host population. Then, Kay et al. (1979) proposed the feeding index, defined as the frequency of mosquitoes that fed on one host with respect to another host, divided by the expected frequency of mosquitoes that fed on these two hosts based on the presence of the considered hosts.

For its part, the human blood index (HBI) is defined as the proportion of mosquitoes that have fed on humans out of the total number of fed mosquitoes (Silver 2008). Although this metric does not consider host availability, it is widely used given its epidemiological relevance as it quantifies the degree of human-vector contact.

Blood meal identification

A bite of history

Blood meal origin can be determined using a wide range of tools that have evolved over time, from the interfacial precipitin test to recent advances in molecular techniques. In general, the analysis of blood meals is most effective in mosquitoes collected within 24 to 72 h post-feeding, period that varies according to the sensitivity of the analytical technique (Gomes et al. 2001; Kent and Norris 2005). The quantity of blood imbibed and the degree of digestion also affect the success of host identification (Martínez-de la Puente et al. 2013).

Serological techniques were first designed for forensic and academic purposes. The pioneering work by Nuttall (1904) was a milestone in identifying blood meals from different animal taxa. However, almost 20 years passed before the precipitin test was adapted to analyze mosquito blood meals. In 1921, Roubaud (1921) postulated the existence of two physiological races of *An. maculipennis* with different feeding habits, one exclusively anthropophilic, and the other zoophilic, more or less definitely preferring animals (sic), and emphasized the epidemiological importance of "animal deviation" in the spontaneous disappearance of malaria. This theory aroused considerable discussion, and a method of precipitin testing of the stomach contents of mosquitoes was used independently in 1922 by Grassi (cited by Missiroli and Hackett 1929) and by King and Bull (1923), and then more broadly by Darling (1925) and Boyd (1930). During the 1930s the precipitin method gained increasing popularity and three decades later, following a World Health Organization initiative, 124.000 tests were carried out on blood meals from 92 *Anopheles* species, largely using antisera directed against humans and domesticated animals (Bruce-Chwatt et al. 1966). Antisera have also been produced for the analysis of blood meals from a wide range of wild animals, especially birds that were known to carry many mosquito-borne arboviruses (Edman 1971; Tempelis 1975).

The precipitin test technique, including variations such as the microplate tests and the agar gel double diffusion test, was mainly used until the development of the enzyme-linked immunosorbent assay (ELISA), in which antigen–antibody reactions are monitored enzymatically. This technique was first used for blood meal identification in the 1980s (Washino and Tempelis 1983; Clements 1999) and was enhanced with the antibody sandwich ELISA by Wirtz et al. (1985). Almost simultaneously, Boreham and Lenahan (1976) developed two techniques to measure the incidence of multiple feeding by mosquitoes. One detects the ABO blood group substances for identifying different human hosts in mosquito blood meals, having relevance in diseases in which the risk depends on the human blood type, e.g. malaria (Chung et al. 2005; Muñoz-Vahos et al. 2012). This system can be used up to 24–30 h after feeding, depending on the mosquito species and is limited by cross-reactions which develop between blood group substances as digestion occurs in the midgut of the mosquito. The second targets serum protein haptoglobins, which can be detected to determine the type of blood in single feeds up to 16–20 h post-feeding (Boreham and Lenahan 1976; Washino and Tempelis 1983).

Despite of the great contributions made in the study of host feeding patterns for over a century, serological techniques have several disadvantages. Most importantly, they require a priori selection of which hosts will be tested and exclude other potential hosts. As some antibodies lack species-level specificity, this results in binding to nontarget species sera and a high percentage of false positives. Also, it is frequently impossible to identify the blood source at the species level due to the lack of specificity for phylogenetically close taxa (Clements 1999).

The arrival of molecular tools

Since the proliferation of molecular tools, a group of techniques for blood meal analysis began to be developed, based mainly on polymerase chain reaction (PCR) and a growing wealth of publicly available DNA sequences, which have achieved successful identification to host species and even to the individual host level (Kent 2009).

Coulson et al. (1990) were the first to perform host DNA analysis using repetitive segments in nuclear genes, aiming at identifying different human hosts in mosquito blood meals. Given that erythrocytes and thrombocytes are anucleated, the amount of DNA in human blood isolated from a fully fed female of *An. gambiae* (around 10 ng) was insufficient for DNA profiling with locus-specific or multi-locus probes. To overcome this problem, PCR was used to amplify certain sequences within the human DNA contained in the blood meal. The study of microsatellite DNA has the advantage of being easily amplified even from partially degraded blood meals due to their small length (Mukabana et al. 2002), and has been applied to uniquely genotyping individual hosts. Allele sizes at multiple loci are characterized to generate a unique profile for each individual, and these profiles are matched to the ones obtained from blood meals to determine heterogeneity in blood feeding patterns. It has been applied mainly for the study of anthropophilic mosquitoes but also for specimens feeding on house finches and domesticated pigs (Darbro et al. 2007; Keven et al. 2019).

Mitochondrial genes have been popular for blood meal analysis. Mitochondria are maternally inherited organelles that contain independent genomes and are present in high numbers (hundreds to thousands per cell). As the mitochondrial genome evolves five to ten times faster than the nuclear genome, it can be employed to resolve broader taxonomic groups and also to distinguish subpopulations within a specific taxon. Cytochrome b (cytb) is the most commonly targeted gene (Kent and Norris 2005; Molaei et al. 2007, 2008), and the cytochrome c oxidase 1 (COI) gene has also been successfully employed with the potential to identify mixed blood meals (Meece et al. 2005; Silver 2008; Kent 2009), and is the target of a large-scale DNA-barcoding project (Reeves et al. 2018b). Ribosomal RNA genes have also been employed for the identification of arthropod blood meals. As with mitochondrial cytochrome genes, the high number of copies of rRNA genes promises robust amplification from minimal starting material. So far, it has been used primarily for ticks (e.g., Pichon et al. 2005).

The most straightforward molecular method for the identification of mosquito blood meals is DNA sequencing; however, its costs can make processing large numbers of samples difficult. This approach is ideal when studying zoophilic arthropods with the potential to feed on many different species of domestic and wild animals, or if the host range of the species under study is unknown. Conserved primers are employed to amplify homologous DNA fragments from diverse potential blood sources, and the obtained sequence is matched to any of those available in open access databases. In particular, the large number of sequences in the GenBank (the most widely used database to share DNA fragments sequenced by users around the world) allows the comparison of the unknown sequence with thousands of potential hosts. If the exact blood meal source is not available in the database, placement in the correct phylum, order, family or genus may be possible from the list of top matches.

Other methods avoid sequencing by amplifying conserved regions for particular taxa based on specific primers in a multiplex-PCR (e.g., Kent and Norris 2005; de Carvalho et al. 2014; Field et al. 2020), or combining PCR with restriction endonucleases that cleave DNA at specific sequences (e.g., Oshaghi et al. 2006). In both cases, differentially sized segments are resolved visually by gel electrophoresis. Less common methods include terminal RFLP and heteroduplex analysis (e.g., Meece et al. 2005; see Kent 2009 for a full description). More recently, matrix-assisted laser desorption/ionization-time of flight (MALDI-TOF)-based methods have been adapted from arthropod species identification to blood meal analysis (e.g., Lee et al. 2015; Main et al. 2016). Using this proteomic tool, one can obtain a mass spectrum protein profile from a crushed engorged abdomen. Such profiles are different depending on the blood meal source, and the mass spectrum from an unknown sample can be compared with a library of spectra from a reference database. Finally, next-generation sequencing (NGS) allows the sequencing of millions of DNA fragments, from thousands of DNA templates in parallel. This technology has been recently applied to the identification of mosquito blood meals with very promising results (e.g., Logue et al. 2016; Reeves et al. 2018b).

State of art in South America

A total of 832 mosquito species are known in South America (WRBU 2021). The varied climatic zones and bioregions of South America promote a unique endemic diversity of pathogens, vectors, and host species. Some vector-borne pathogens have a limited host range, as is the case of yellow fever virus which circulates exclusively among primates (Monath and Vasconcelos 2015), while others replicate in a large number of hosts such as West Nile Virus that infects over 400 documented species including humans, birds, horses, amphibians and reptiles (Root 2013; Saiz et al. 2021). Mosquitoes that are able to switch hosts are known as bridge vectors, as they can transmit a given pathogen across taxa. As we have described in the “Host feeding and host preference patterns” section, host availability and environmental conditions are postulated to play a key role in determining spatiotemporal variations in mosquito feeding habits. Therefore, each vector-host pair may present a particular behavior in different regions and, as we shall see in the “South American studies” section, our understanding of these interactions in South America remains poor for most species.

Mosquitoes regionally relevant as vectors

Among the wide range of mosquito-borne diseases in South America, some are endemic (e.g., yellow fever), whereas others have been accidentally introduced and are considered emerging in the continent (e.g., Zika fever). Certain diseases present a unique or limited range of vectors, as opposed to others that can be transmitted by several mosquito species and even genera (Weissenbock et al. 2010).

Anopheline mosquitoes are vectors of malaria, which is caused by protozoa of the genus *Plasmodium.* Transmission varies regionally depending on climate and biogeography, and is exacerbated by anthropogenic activities such as deforestation, mining, and dams, which create new larval habitats, and promote human mobility to areas with little public health infrastructure. In South America, most cases occur in the Amazon rain forest of Venezuela, Brazil, Colombia, Peru, and Guyana, with an estimated incidence of up to 44 per 1000 people at risk in 2018 (Roser and Ritchie 2019). The main mosquito species involved in the region are *An. darlingi*, *An. nuneztovari*, *An. aquasalis*, and *An. albitarsis s.l.* (Rodríguez 2006; Laporta et al. 2015).

Aedes aegypti is a highly domesticated species, now considered endemic to South America after its introduction via ships in the 1400s (Powell et al. 2013). It is currently a prominent vector of dengue (DENV), Zika (ZIKV), and chikungunya (CHIKV) viruses transmitted throughout the continent. Dengue virus is regionally hyperendemic, with cyclic epidemics occurring every 3 to 5 years (Murray et al. 2013). Highest incidence rates were reported in 2019 in several countries with Brazil at the top of the list (> 2 million cases; WHO 2019). Zika virus was first identified in South America in Brazil during 2015, and after a quick spread it has been confirmed as a cause of congenital abnormalities and as a trigger of Guillain-Barré syndrome, prompting intensified surveillance and control efforts (Borchering et al. 2019). For its part, over one million cases associated to CHIKV have been reported in the Americas since its first detection in 2013.

Aedes aegypti is also the urban vector of yellow fever virus (YFV). Despite the availability of an effective vaccine it is still a public health concern because fatality rate can reach 50% among symptomatic cases (Chen and Wilson 2020). This zoonotic disease circulates in a sylvatic cycle in forested areas among non-human primates. The main vectors are *Haemagogus janthinomys* and *Hg. leucocelaenus*, but other *Haemagogus* (4 species), *Sabethes* (5), *Aedes* (3), and *Psorophora* (2) have also been characterized as locally important vectors (Segura et al. 2021). In relation to this, *Haemagogus* and *Sabethes* mosquitoes are also considered candidate vectors for a potential sylvatic ZIKV cycle in the New World (Karna et al. 2018).

Aedes albopictus has been proven a competent vector of DENV, ZIKV and CHIKV in experimental conditions, although so far it has been found infected in the field only with DENV (reviewed in Jones et al. 2020). This invasive species was restricted to Asia until its introduction to the Western Hemisphere probably through shipments of used tires near 1985 in USA and Brazil (Lounibos 2002). Its aggressive diurnal habits and potential role as a bridge vector increase its epidemiological relevance.

Several species belonging to the genus *Culex* have been incriminated as main vectors of different Flaviviruses in the region. The enzootic transmission cycles of West Nile virus (WNV) and Saint Louis encephalitis virus (SLEV) involve *Culex* mosquitoes and birds, whereas humans and other mammals are considered dead-end hosts in the epizootic cycle. WNV was introduced to North America in 1999 and took only two years to spread to South America. In contrast to other regions, human cases have been scarce and bird/equine mortality rates low (Díaz et al. 2011; Batallán et al. 2020). For its part, SLEV is distributed exclusively in the American continent. Although information in South America is practically zero, in central Argentina *Cx. quinquefasciatus* and *Cx. interfor* mosquitoes have been characterized as part of the cycle. Other mosquitoes of the genera *Aedes*, *Anopheles*, and *Psorophora* have also been detected infected during enzootic periods (Díaz et al. 2012).

Rocio virus (ROCV) is an epidemic flaviviral disease first observed in São Paulo State, Brazil, in 1975. *Psorophora ferox* was the only mosquito species directly implicated in transmission through virus detection in field-collected specimens, but *Cx. tarsalis* and *Cx. pipiens* mosquitoes have been proven relatively efficient experimental vectors (Mitchell 2001). Other viruses of the genus Alphavirus which is also present in South America are eastern equine encephalitis virus (EEEV), western equine encephalitis virus (WEEV), Venezuelan equine encephalitis virus (VEEV), and Mayaro virus (MAYV). Eastern equine encephalitis virus causes sporadic epizootics of varying magnitude in Argentina, Brazil, Venezuela, and Colombia, producing encephalitis with 30–40% mortality rate in humans and 80–90% in equids (Go et al. 2014). Mosquitoes of the genera *Culex* (*Melanoconion*), *Culiseta*, *Aedes* (*Ochlerotatus*), and *Coquillettidia* have been postulated as vectors of enzootic cycles (Lehane 2005; Contigiani et al. 2016). Western Equine Encephalitis Virus is extended throughout South America, causing mainly small equine epizootics. It is maintained in an enzootic cycle between passerine birds and mosquitoes of the genus *Culex*, while lagomorphs and rodents are thought to serve as amplification hosts when they are infected by *Aedes* mosquitos (Go et al. 2014). The enzootic cycle of VEEV involves *Culex* (*Melanoconion*) mosquitoes and small rodents as hosts, whereas *Aedes* and *Psorophora* mosquitoes participate in epidemic and epizootic cycles. Equids may act as amplifying hosts by developing high levels of viremia, with 40–60% morbidity and 50% of the sick dying. In humans, enzootic strains generally produce mild symptoms, while infection with epizootic viruses can be severe (Weaver et al. 2004; Contigiani et al. 2016). Mayaro Virus has been isolated from humans in seven South American countries. The sylvatic cycle could be similar to that of YFV, involving wild primates and *Haemagogus* mosquitoes, although *Ae. aegypti* and *Ae. albopictus* were experimentally infected and some species of *Culex*, *Sabethes*, *Mansonia*, and *Psorophora* were found naturally infected (Ganjian and Riviere-Cinnamond 2020).

Bunyamwera orthobunyavirus (BUNV) virus was also detected in the continent in horses and humans, and recovered from *Ae. albifasciatus*, *Ps. varinervis*, *Cx. intrincatus*, *Cx. acharistus*, and *Cx. educator* (Tauro et al. 2015; Gallardo et al. 2019). Other related viruses affecting humans, as Cache Valley virus (CVV), were also found infecting *Ae. albifasciatus* and *Ps. varinervis* (Sabattini et al. 1998; Tauro et al. 2009).

Regarding filariae, the best-known example of vertebrate parasites is *Wuchereria bancrofti,* responsible for lympathic filariosis. In South America, it remains endemic to Brazil and Guyana and is mainly vectored by *Anopheles* species and *Cx. quinquefasciatus*; humans are the main hosts (Lehane 2005; CDC 2021). Another filarial disease is the dirofilariasis, a parasitic zoonosis caused by nematodes of the genus *Dirofilaria*, being *Dirofilaria immitis* the most relevant and widely distributed. This parasite has been detected in almost all South American countries; it infects domestic animals and a wide range of wild animals (Anderson 2000; Vezzani and Eiras 2016). A large number of species of the genera *Aedes*, *Culex*, *Anopheles*, *Psorophora*, and *Wyeomyia* have been incriminated as vectors in different regions of the continent (Vezzani and Eiras 2016).

South American studies

Data collection

We compiled information available until the end of 2020 from research articles and thesis in Web of Science, Scopus, PubMed, Scielo, Google Scholar, Research Gate and Latin American Repositories Network by using the following search terms: bloodmeal, blood meal, bloodmeal identification, bloodmeal mosquitoes, culicidae, host, host feeding, host feeding patterns, host-mosquito, host preference, host selection, mosquitoes, mosquito feeding, vector, vector-host, their equivalents in Spanish and Portuguese, and the scientific name of the mosquitoes well-known as vectors (e.g., "*Aedes aegypti*"). The reference lists from all compiled articles were also examined to identify any further relevant paper.

The following information was extracted from each study: country, study type, number of individuals analyzed for each mosquito species, and host identification (hereafter ID) up to the maximum taxonomic detail available. Study types were classified as follows: human bait as collection method, host ID by specimens collected in baited traps (either engorged or not), and blood meal ID by serological or molecular techniques, including details about host availability estimation if informed. Studies using human bait as collection method were included despite no specific objective regarding feeding habits was raised, given that they provide valuable information about anthropophilic species, particularly in countries that lack specific studies.

The geographic distribution of the mosquito species across South America were added to the dataset extracting the records of the Walter Reed Biosystematic Unit (WRBU 2021), with the exception of Argentina, for which a more comprehensive checklist was used (Rossi 2015). In addition, a species was added for a given country if a study mentioned it among the collected specimens, e.g., *An. albitarsis* in Guyana (Giglioli 1963), *Cx. eduardoi* in Brazil (Barbosa et al. 2003), and *Ur. pallidoventer* in Bolivia (Roberts et al. 1985).

The blood feeding habit of each mosquito species was categorized based on a comprehensive analysis of the information compiled. A broad first qualitative approach provided the list of hosts for each mosquito species categorized as human, other mammals, bird, reptile, amphibian, and their combinations. Then, a detailed assessment was performed for those mosquito species best represented in terms of number of individuals and publications. Finally, an additional interpretation was performed using exclusively those works that considered host availability.

Regarding the taxonomic detail of the mosquito species, all the information was included even if reported as group of species, at genus or subgenus level. In vacant gaps, such as *Culex* (*Microculex*), host feeding data at subgenus level could provide valuable cues. Taxa recorded at genus or subgenus level were not considered in analyses related with species numbers. In the case of species groups, they summed to the total species number only if no information regarding the individual members of the group was available. For those studies that did not include the number of specimens analyzed, the host ID was considered only qualitatively.

Results

Available data We found 147 scientific articles, one PhD thesis and four Master thesis that report information on different aspects of mosquito feeding habits across ten of the 13 South American countries, from 1928 to 2019 (Fig. 1; Table S1). The information is highly unbalanced among countries, both in the number of researches and species involved. The overwhelming majority of the studies were carried out in Brazil (76), followed by Colombia (22) and Peru (16). To our knowledge, no information is available for Chile, Paraguay, and Uruguay. Among the bibliography compiled, 122 researches focused on one or several mosquito-borne diseases. Malaria was by far the most common aim of the investigations (99), followed by SLEV and/or WNV and/or YFV (7), VEEV/canine dirofilariasis (6), WEEV (4), and EEEV/ROCV/avian malaria/lymphatic filariasis (2). During the past century all studies consisted in human landing collections, baited traps or blood ID by serological methods, and it was not until 2009 that studies using molecular tools appeared (Fig. 2).

Among 832 mosquito species recorded in South America (WRBU 2021), only for 246 (29.5%) there is some information regarding their blood feeding habits. In other words, there are 586 species known in the continent without any

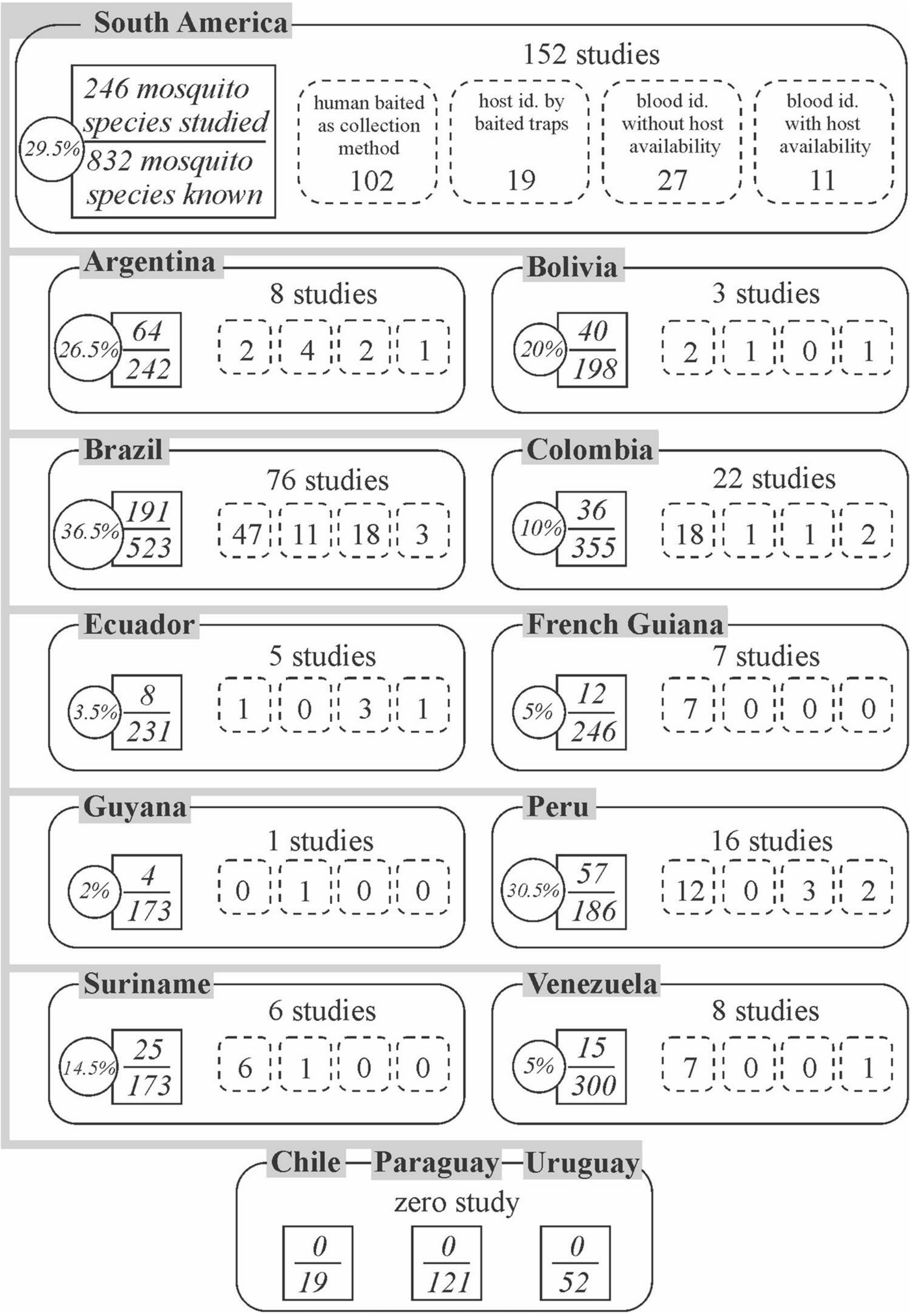
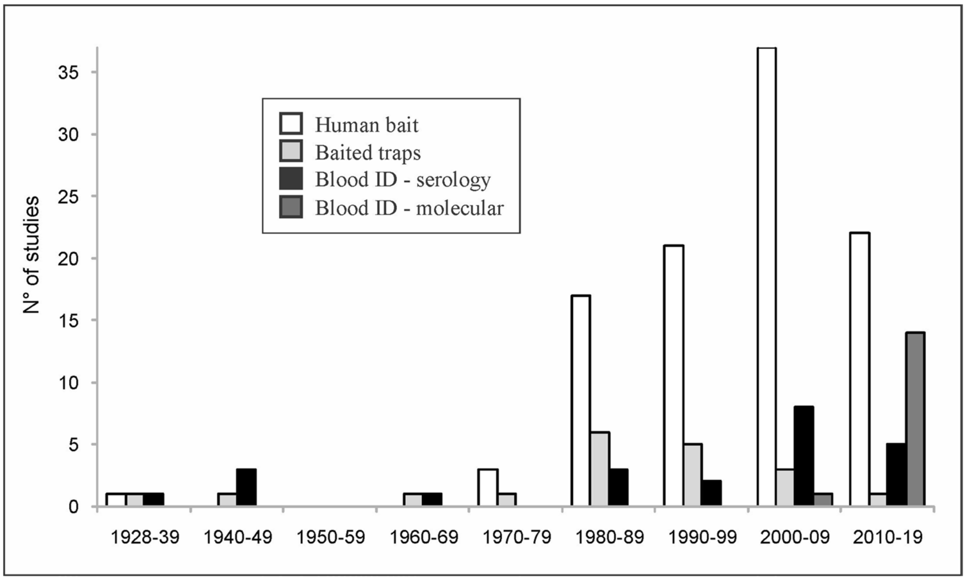


Fig. 1 Available scientific studies related with blood feeding habits of mosquitoes in South America; number of researches by study type within dashed boxes and percentage of mosquito species studied within circles

data about which hosts they feed on. Brazil presented the highest number of species investigated (191) and the highest percentage of its culicid fauna studied (36.5%), comprising 20 genera, whereas others such as French Guiana, Guyana, and Venezuela focused on very few species of one genus (Fig. 1; Table S1). The majority of the studies reported results on *Anopheles* species, sometimes for one or two species and others for the entire assemblage. In general terms, 24 studies focused on a single mosquito species, 38 studies dealt with two to five species and the remaining 90 researches provided information on the entire mosquito assemblage.

Only 53 of the 152 studies compiled could be considered formally as host feeding investigations (i.e., host ID by baited traps or blood ID of field collected specimens) whereas 99 solely contribute to the list of anthropophilic species detected using human bait as mosquito collection method for other purposes. Some studies used simultaneously two

Fig. 2 Number of studies per decade related with blood feeding habits of mosquitoes in South America by study type



approaches, e.g., two researches collected mosquitoes by human bait to study daily biting activity and also used baited traps to assess host preference. Host ID by baited traps was used in 19 studies across six countries whereas blood meal ID of field collected mosquitoes was used in 38 studies of seven countries (Fig. 1). Among the latter, 23 applied serological methods and 15 included molecular tools (Table S1).

The feeding status of mosquitoes collected in baited traps was considered only in four studies (Mitchell et al. 1985, 1987; Almirón and Brewer 1995; Stein et al. 2013). Freshly engorged mosquitoes (i.e., containing red blood in their abdomen) could be assumed to have fed within the animal bait, whereas non-engorged mosquitoes may have been only attracted to the trap device itself or the host in it. Independently of the animal used as bait in these studies (horse, chicken, rabbit, toad, and turtle), authors found that engorgement rates vary among baits depending on mosquito species, suggesting important differences in the interpretation of data between attracted and fed mosquitoes.

Within baited trap and blood ID investigations, the assessment of seasonal and inter-annual variations of feeding habits is almost absent. Only Stein et al. (2013) included a study design that allowed for the detection of changes in the host preference of a mosquito assemblage among seasons. Similarly, only Moreno et al. (2017) compared inter-annual changes of the host choice and stressed seasonal variations of HBI, contributing with valuable data on seasonal changes of feeding patterns on humans. Other approaches were the inclusion of intra- versus peridomicile (35 researches) and the comparison of different environments as for example urban/rural/wild (19).

Of the 246 mosquito species with available information, 172 species were formally studied by baited traps or blood ID and for the remaining 74 data is restricted to human landing collections (Table S2). Most species were only studied in one or two countries and very few have been studied throughout the continent (Fig. 3A). Similarly, considering their geographic distributions (see Table S2 columns B and C), the majority of the species were investigated in up to 1/3 of their distribution range (Fig. 3B). In general terms, the bulk of species were involved in only one to three investigations and few were deeply studied (Fig. 3C). Species most frequently studied (> 30 publications) were those of the genus *Anopheles* incriminated in malaria transmission. Surprisingly, other relevant vectors such as *Ae. aegypti*, *Ae. albopictus*, and *Hg. janthinomys* were hardly studied, and many species suspected as vectors of little-known diseases barely were involved in one research, e.g., *Cx. acharistus* and *Cx. educator*. In brief, 59.6% of the species were studied only in one country, 64.6% of the species were studied in a narrow range of their distributions, and 34.6% of the species were involved in only one research.

Overall, the pooled dataset summed more than 1.6 million mosquitoes; 1,518,730 in human landing collections, 144,779 in baited traps, and 24,904 in field collected mosquitoes for blood ID. As expected, the total numbers of specimens per species were also unbalanced. Those *Anopheles* involved in more researches were also by far best represented in terms of number of specimens, with four species accounting for 73% of the total. On the other extreme, only one specimen was analyzed for some species like *Cx. lopesi* and *Ur. nataliae* (Table S2).

Finally, an evaluation of host availability in order to estimate mosquito host preferences in field conditions was conducted in 11 studies (Table S3). Ten of them quantified host availability at mosquito capture sites, by one or a combination of the following tools: census of individuals providing absolute counts (e.g., Gomes et al. 2003; Bataille et al.

2012), visual, and/or auditory sampling of avian species (e.g., Mendenhall et al. 2012; Hoyos Loaiza 2018), surveys to residents (e.g., Rubio-Palis et al. 1994), and bibliographic sources or data bases available for the area (e.g., Alencar et al. 2005). The obtained information was used considering the raw number of individuals (in the majority of the studies) or standardized by animal weight (e.g., Lardeux et al. 2007; Saavedra et al. 2019). The most widely used metrics were the feeding index and the forage ratio, whereas a particular study employed species interaction networks (Hoyos Loaiza 2018). Additionally, one study fixed host availability in an experimental design by offering simultaneously one individual of human, dog, cat, pig, ram, bull, horse, and chicken and then testing the ingested blood by precipitin (Deane et al. 1949).

Blood feeding habits Table S2 details the findings regarding blood feeding habits for all mosquito species studied, considering all researches and techniques. At least 223 species could be described as anthropophilic as they were captured in human landing collections, either as part of baited traps experiments or for other research purposes. Other four species were added to the anthropophilic list by blood ID of field collected specimens. Among these 227 species, 56.9% were also attracted and/or fed on others mammals, birds, reptiles and/or amphibians (Fig. 4A; column J in Table S2). Some of these species (6.1%) are clearly generalist/opportunist, feeding on every vertebrate taxa considered, whereas others (15.1%) feed exclusively on non-human mammals. This first approach, although biased by human landing collections, provides candidates to act as bridge vectors of zoonotic diseases involving birds and/or mammals, and as vectors in sylvatic maintenance cycles. Equally important, these results highlight the lack of data for assumed vectors of some diseases; e.g. *Ae. aegypti* was only recorded to feed on humans despite it has been incriminated in the transmission of the dog heartworm *D. immitis* (Vezzani and Eiras 2016).

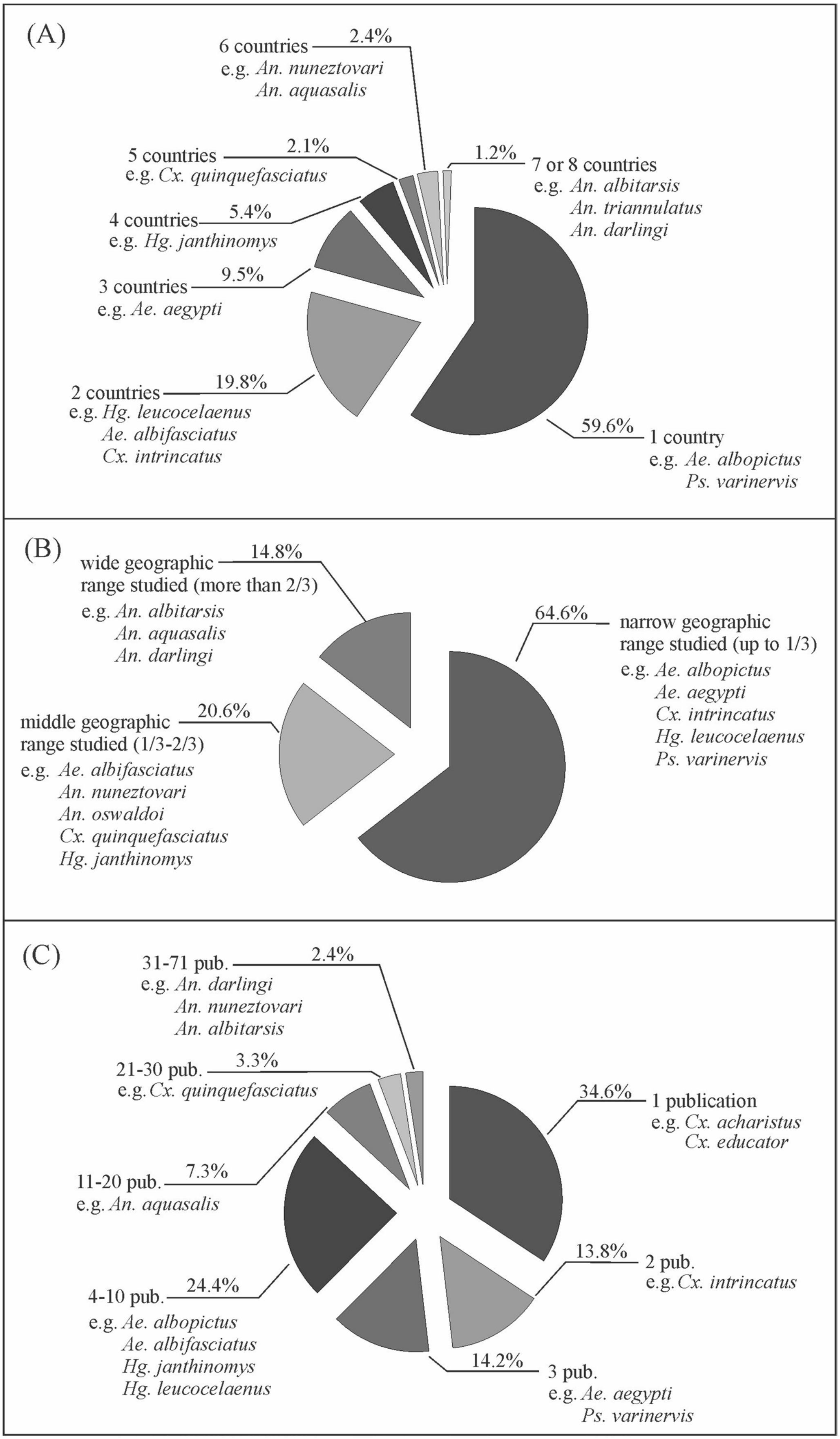
Data from the subset of 19 researches that used baited traps includes 143 mosquito species, of which 83.9% were attracted to humans, 10.5% exclusively and 73.4% in combination with other hosts (Fig. 4B; column K in Table S2). The remaining 16.1% of the species were attracted to other mammals (9.1%), birds (0.7%), both (4.9%), or in combination with reptiles and amphibians (1.4%). This information is biased by the choice of bait vertebrate taxa depending on the aim of each study; e.g. five mosquito species were attracted by reptilians and/or amphibians when offered, but this setting was only tested by Almirón and Brewer (1995). Anyway, these publications contribute with valuable information about host choice among human-bird-mammal. However, as we shall see in the next paragraph, host feeding patterns in natural conditions do not necessary resemble baited traps field experiments.

The 38 investigations focused on host blood ID of field collected specimens provide data on 102 mosquitoes species. A total of 60.8% of these species fed on humans; 4.9% exclusively and 55.9% in combination with other hosts (Fig. 4C; column L in Table S2). Unlike in baited traps findings, several mosquito species (12.7%) included in their diets all vertebrate taxa (except fish) besides humans. A great percentage of the species (39.2%) were found exclusively with non-human ingests; 10.8% exclusively birds and 13.7% exclusively mammals, 9.8% both and the remaining 4.9% including also reptiles and amphibians.

The comparison of the findings between baited trap and blood ID studies shows that the percentage of mosquito species identified as anthropophilic (exclusively or not) is higher in baited traps, whereas the identification of reptiles, amphibians, and non-human host categories is higher in blood ID of field collected mosquitoes (Fig. 4B versus 4C). Among 73 mosquito species assessed by both methods, only 17 yielded similar results (Table S2, columns K and L). In the other cases, host lists are complemented by both methods. For example, baited traps added human/reptile/amphibian as hosts for *Ae. albifasciatus* and human/other mammals for *Cx. intrincatus*, whereas blood ID added bird as host for *Ae. albopictus* and *An. darlingi*. In general, baited traps added human (for 17 species) whereas blood ID added birds, reptiles and/or amphibians (for 26 species) to the host list. It is worth noting the importance of human landing collections in making the list of anthropophilic mosquitoes, i.e., the human host data comes exclusively from this bibliographic source for 93 mosquito species.

Detailed information about the number of individuals processed in baited traps and blood ID studies for each mosquito species (Table S2, columns F–H) allow to perform a quantitative assessment for several species, some of them recognized as important vectors. We exemplified the changes of the observed patterns between baited traps and blood ID methodologies for some well represented *Anopheles*, *Aedes*, *Culex* and *Mansonia* species (Figs. 5 and 6). For all species a dissimilar pattern in terms of host composition and proportions was observed. Additionally, an example of one species each of the genera *Psorophora*, *Wyeomyia*, and *Limatus* studied only by baited traps is presented (Fig. 7). In all cases, mosquitoes were attracted to humans, others mammals and birds, highlighting their potential role as bridge vectors of diseases.

Collectively, the 11 studies that evaluated host availability provided information on the host preferences in field conditions of 31 mosquito species (Table S3). More than 80% corresponded to specimens from nine species of the genus *Anopheles*, with *An. darlingi* accounting for the majority of the individuals followed by *An. aquasalis*. About half of the


(A)
6 countries 2.4%
e.g. An. nuneztovari
An. aquasalis
5 countries 2.1%
e.g. Cx. quinquefasciatus
1.2% 7 or 8 countries
e.g. An. albitarsis
An. triannulatus
An. darlingi
4 countries 5.4%
e.g. Hg. janthinomys
3 countries 9.5%
e.g. Ae. aegypti
2 countries 19.8%
e.g. Hg. leucocelaenus
Ae. albifasciatus
Cx. intrincatus
59.6% 1 country
e.g. Ae. albopictus
Ps. varinervis
(B)
wide geographic range studied (more than 2/3) 14.8%
e.g. An. albitarsis
An. aquasalis
An. darlingi
64.6% narrow geographic range studied (up to 1/3)
e.g. Ae. albopictus
Ae. aegypti
Cx. intrincatus
Hg. leucocelaenus
Ps. varinervis
middle geographic range studied (1/3-2/3) 20.6%
e.g. Ae. albifasciatus
An. nuneztovari
An. oswaldoi
Cx. quinquefasciatus
Hg. janthinomys
(C)
31-71 pub. 2.4%
e.g. An. darlingi
An. nuneztovari
An. albitarsis
21-30 pub. 3.3%
e.g. Cx. quinquefasciatus
34.6% 1 publication
e.g. Cx. acharistus
Cx. educator
11-20 pub. 7.3%
e.g. An. aquasalis
13.8% 2 pub.
e.g. Cx. intrincatus
4-10 pub. 24.4%
e.g. Ae. albopictus
Ae. albifasciatus
Hg. janthinomys
Hg. leucocelaenus
14.2% 3 pub.
e.g. Ae. aegypti
Ps. varinervis

◂**Fig. 3** Percentage of mosquito species for which their blood feeding habits in South America were studied according to **A** the number of countries, **B** the proportion of their geographic range, and **C** the number of publications in which they were investigated. All percentages were calculated over the total of mosquito species with available information in the continent (i.e., 246)

species, covering all considered genera, were classified as mammophilic including human as host. Of the remaining, ten were classified as opportunistic, feeding in most cases from mammals and birds, and only two *Culex* species were ornithophilic. It is worth noticing the report of *Ur. lowii* which fed preferably on amphibians. For *Cx. nigripalpus*, results from two Brazilian studies were discrepant; opportunistic according to Gomes et al. (2003) and mammophilic including human according to Alencar et al. (2005). The host preferences of the other five species which were reported in more than one study were concordant. For some species studied only in Hoyos Loaiza (2018), reported host preference would be inconclusive due to low number of specimens analyzed ($n<6$).

Finally, the comparison of pooled data extracted from Table S2 and host preferences from Table S3 highlights the importance of carefully assessing what information each type of research provides. For example, species identified as mammophilic such as *Ae. albopictus*, *An. albitarsis*, *Cx. quinquefasciatus*, and *Ma. titillans* also fed on birds, and ornithophilic mosquitoes like *Cx. saltanensis* also fed on mammals. The role of each mosquito vector in the transmission of a disease will depend on both the intrinsic feeding preference and the availability of its potential hosts in a given place and time.

Conclusions and final comments

Research on mosquito feeding habits provides insight in vector-host interactions, which are essential for disease transmission. As was stressed in previous sections, female mosquitoes of most species require a blood meal to complete their gonotrophic cycle, thereby transmitting blood-borne pathogens. Although rooted on a genetic basis, host feeding also depend on local ecological factors like host availability and abundance, habitat, and climatic conditions (Asigau et al. 2019). For 70% of the mosquito species reported in South America, there is absolutely no information regarding what they feed on, and the majority of the remaining species have been investigated in a limited range of their geographic distribution. The genus *Anopheles* was the most widely studied in terms of publications, number of individuals and geographic scope. Remarkable vacant gaps are the little information about well-known vectors of diseases such as *Ae. aegypti*, *Ae. albopictus*, and *Culex pipiens s.s.*, and also on species considered responsible of sylvatic cycles of YFV, as *Haemagogus* and *Sabethes* mosquitoes. The maintenance of enzootic cycles are, in part, the reason why vectorial disease eradication campaigns generally fail. Species from several genera could act as bridge or maintenance vectors of poorly known or currently emerging diseases.

Beyond the outstanding leadership of Brazil, the scarcity of investigations and species studied in the majority of the countries of the region is remarkable. In Chile, Paraguay, and Uruguay, there is no data about blood feeding habits of any mosquito species, and in others only a few *Anopheles* species were barely investigated. Contrary to the logic of considering human landing catches a disused methodology for ethical issues, it has been the most widely used approach until the present. Serological ID of blood fed mosquitoes collected in the field increased during 2000–2009, presumably driven by the switch from precipitin to ELISA techniques. Despite molecular studies are currently trendy, in South America, their contribution is still incipient and is expected to rise sharply in the near future. Both available methods, serological and molecular, are valuable but clearly should be used according to the main goal of the research. If it is to understand feeding patterns on a single host at risk, such as humans, serological methods can be useful. However, if the aim is to report a broad spectrum of hosts up to species levels, PCR amplification of conserved regions followed by sequencing is unavoidable.

Human landing collections contributed with the identification of many mosquito species attracted to humans. From the list of suspected anthropophilic mosquitoes, more than half were also attracted and/or fed on other vertebrates, providing cues for future researches on specific diseases transmission cycles. Regarding animal bait studies, amphibians and reptiles were mostly excluded by investigators due to their apparent low epidemiological relevance in human diseases. Despite this, baited traps made huge contributions about host choice among birds, humans and other mammals, improving the comprehension of the transmission of mosquito-borne diseases that affect humans. However, a trap could be attractive itself by acting as refuge or resting place, and also an animal used as bait could attract specimens that finally do not feed on it. For such reasons, the information provided by studies that report engorged specimens (e.g., Mitchell et al. 1985) could be considered of better quality, or at least of higher certainty. Those studies that assessed the proportions of engorged specimens in different animal baits (e.g., Stein et al. 2013) suggests dissimilar interpretations of host preference when comparing the total number of attracted mosquitoes and the proportion of actually fed individuals.

It is unavoidable to ask oneself if host choice reported in baited trap studies is representative of natural feeding behavior of mosquito specimens, given the fact that hosts

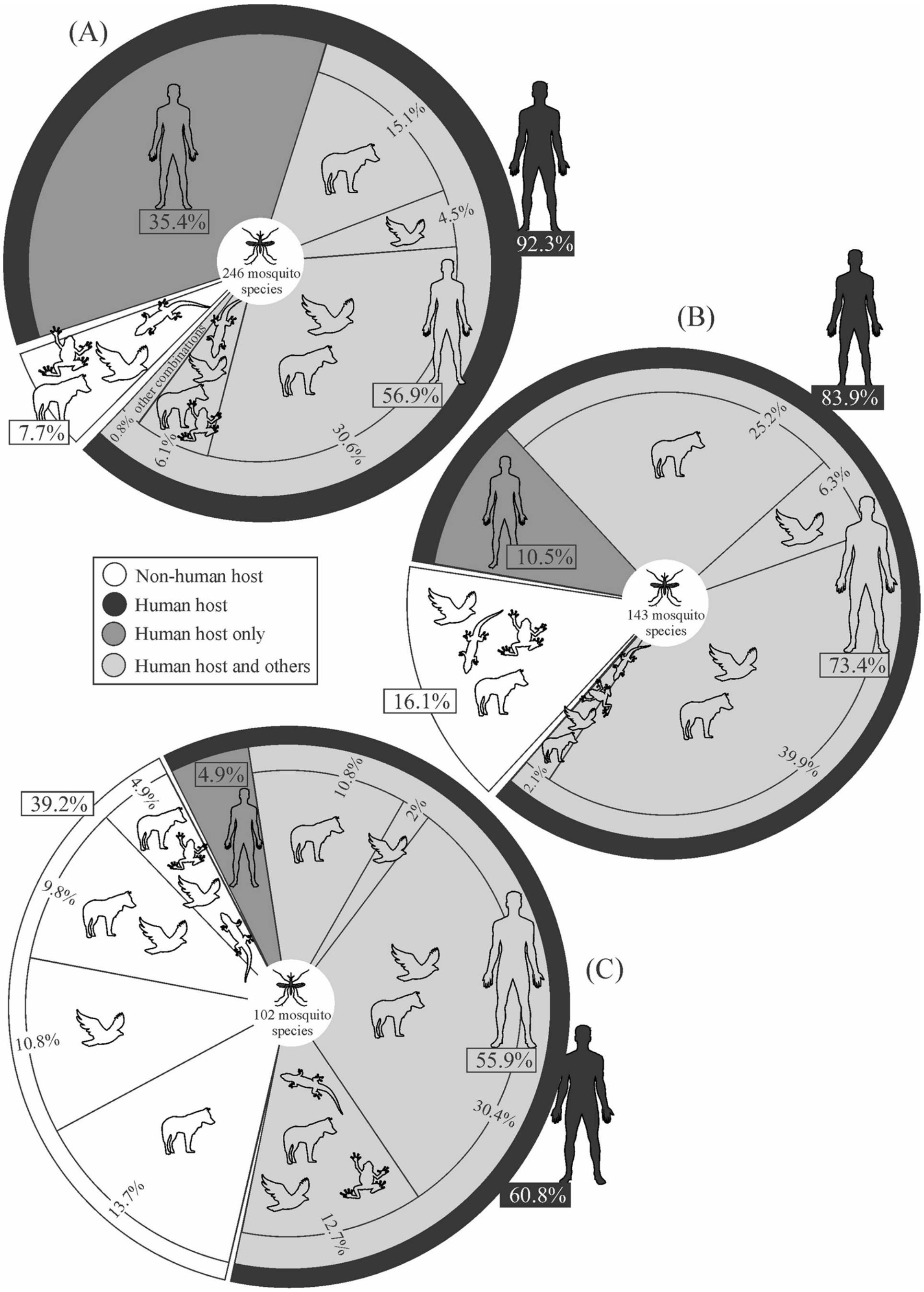
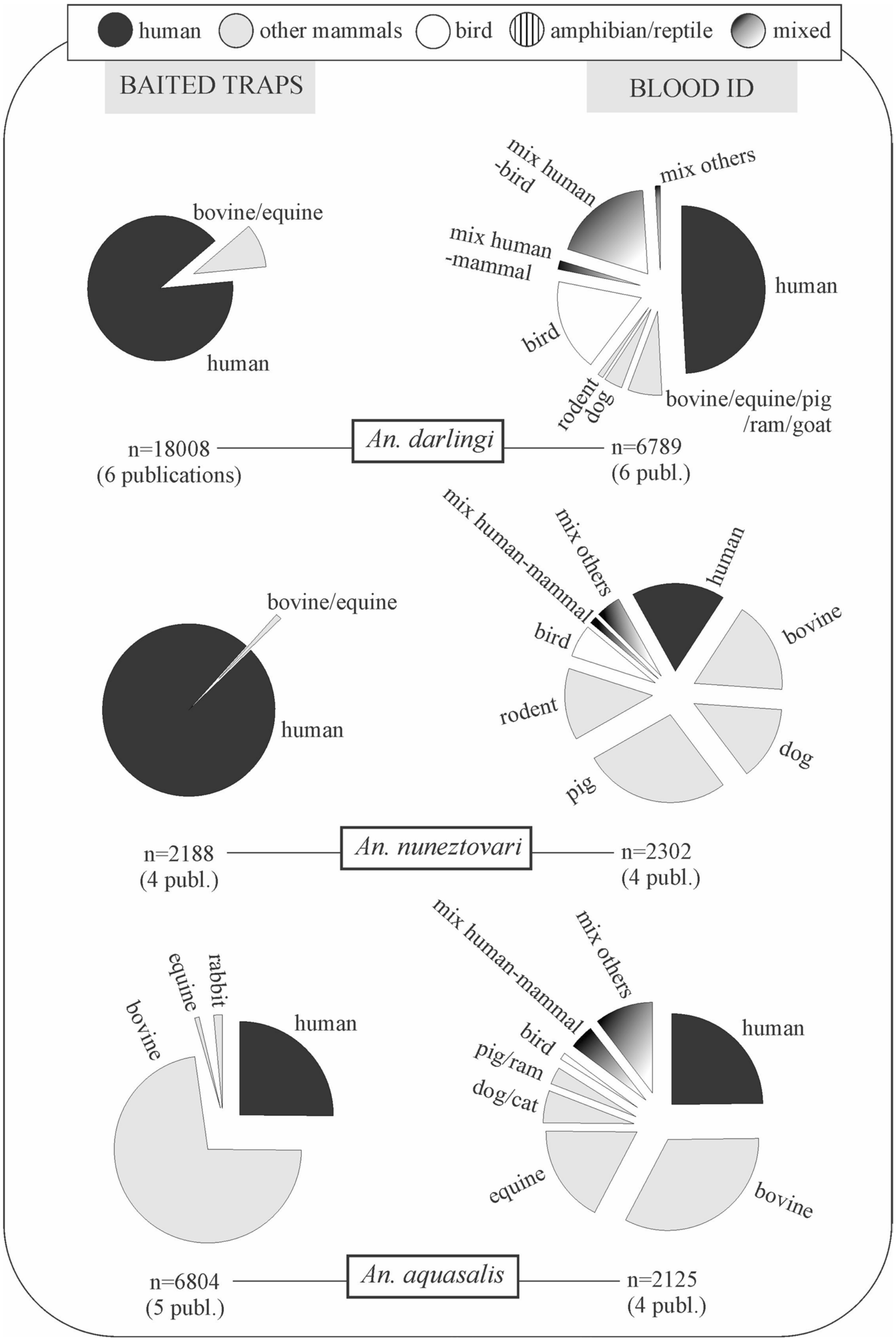


Fig. 4 Blood feeding habits of mosquito species in South America considering pooled data of **A** human landing collections, baited traps, and blood ID of field collected mosquitoes (246 species); **B** only baited traps (143 species); and **C** only blood ID of field collected mosquitoes (102 species)

are, by definition, trapped, highly available and unable to escape. The comparison of results between baited traps and blood ID of field collected mosquitoes performed herein strongly suggests that in natural conditions mosquitoes feed on a wider range of taxa. These differences in feeding habits observed for many mosquito species according to the methodology employed is probably the most substantial finding of the present review. However, it is important to highlight that baited traps also increased host diversity for several mosquito species. In consequence, these methodologies are clearly complementary and, ideally, both should be performed when pursuing a comprehensive study about what mosquitoes prefer and what they really bite.

The importance of considering the relative abundance of hosts to interpret mosquito host preferences was already stressed in late 1960s (Hess et al. 1968). Anyhow, the way in which such host availability estimation is performed is highly relevant. All methods are imperfect, each with different forms of bias and error. Furthermore, a general description of host availability does not resolve other issues, as the ones pointed by Edman (1971) discouraging the use of feeding metrics. The first is regarding which acceptable

Fig. 5 Comparison of host composition and proportions observed by baited traps and blood ID for *An. darlingi*, *An. nuneztovari*, and *An. aquasalis*



(meaning available and attractive) host is closest to a mosquito specimen when and where it searches for a blood meal. This distance is impossible to assess and, although associated, cannot be derived directly from host density. The second reason is the varied flight patterns of mosquitoes from different species in relation to the environment. Some species seem reluctant to leave their preferred habitat even in the search of blood, whereas others travel larger distances in the open during host-seeking. Also, some abundant hosts may be inaccessible for reasons other than density (e.g., within burrows, tree nests, or houses during mosquito feeding) or may present intense defensive behavior. Finally, the degree of concurrence of host and mosquito activity hours is crucial for their encounter. All this said, feeding metrics suggest host preference or avoidance but cannot prove it. They can, however, make blood meal analyses more generalizable

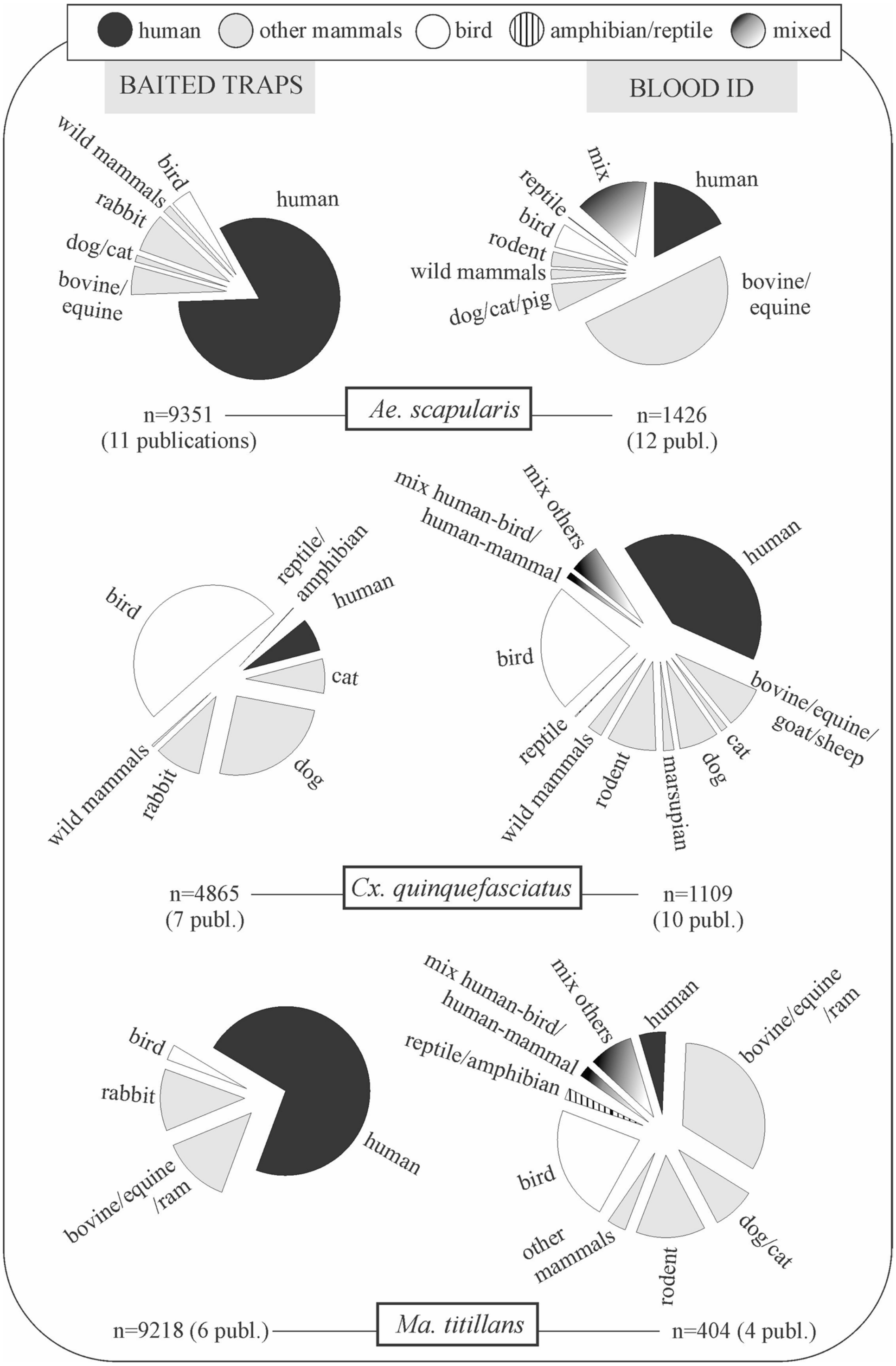


Fig. 6 Comparison of host composition and proportions observed by baited traps and blood ID for *Ae. scapularis*, *Cx. quinquefasciatus*, and *Ma. titillans*

by providing additional host context, therefore enabling more robust conclusions (Fikrig and Harrington 2021).

It is worth highlighting that a poorly selected host could be notwithstanding of high epidemiological relevance if it is part of a transmission cycle, and could be indeed an important component of a mosquito species diet if it is present in high abundance in the environment. The question Which is the host preference of a mosquito species? can be answered by baited trap experiments or by the identification of engorged field collected specimens coupled with host availability estimation, whereas What do mosquitoes of a given species feed on? does not rely on host availability but requires blood identification of a large amount of specimens to capture both abundant and scarce food items. Although

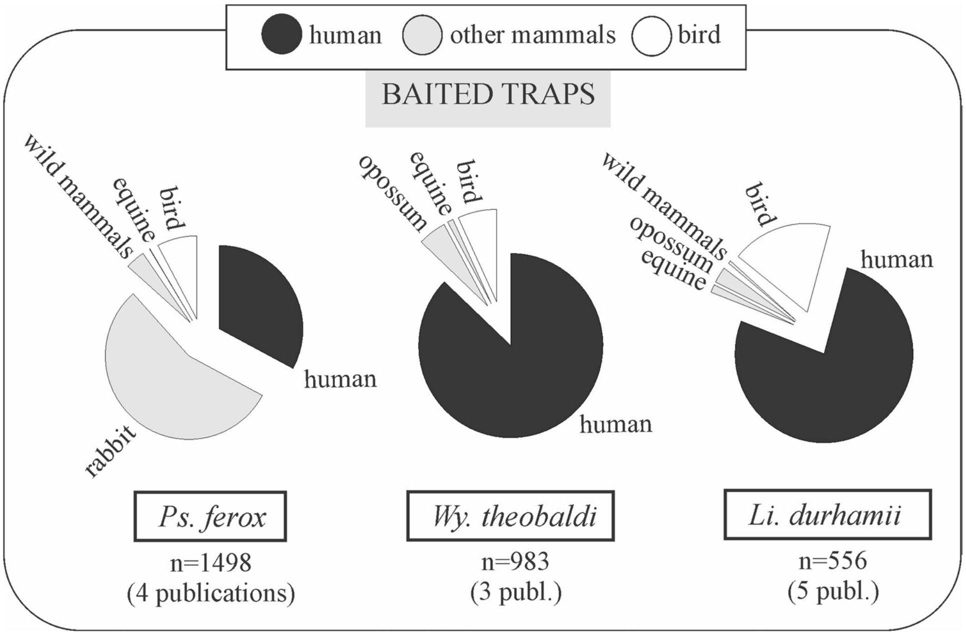


Fig. 7 Host composition and proportions observed by baited traps for *Ps. ferox*, *Wy. theobaldi,* and *Li. durhamii*

both approaches provide different and complementary information, the latter is presumably of higher epidemiological relevance. Whether mosquitoes feed, even infrequently, on non-preferred hosts that may be pathogen reservoirs is key information for pathogen transmission (Fikrig and Harrington 2021).

Finally, the detailed data compiled in Tables S1 and S2 were thought to serve as a guide for future investigations. We hope that the present review encourages mosquito researchers to cover the huge gaps of information regarding what mosquitoes prefer and what they really bite in South America.

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Declarations

Conflict of interest The authors declare no competing interests.

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