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Phlebotomine Sand Flies (Diptera: Psychodidae) of Endemic Foci of Leishmaniosis in Guatemala

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Abstract—In Guatemala, three million people are at risk of contracting cutaneous leishmaniosis, primarily in the northern regions. Despite this alarming epidemiological situation, few faunistic studies of phlebotomine sand flies have been conducted in this country, which is the most populous in Central America. An entomological survey of phlebotomine sand flies was carried out from March to September, 2018 in rural, mountainous, and forested areas of six northern Guatemalan departments with active transmission of human leishmaniosis: Petén, Huehuetenango, Quiché, Alta Verapaz, Izabal, and El Progreso. CDC miniature light traps were deployed in and around homes with recent cases of leishmaniosis in children under 10 years of age. A total of 2,605 specimens of sand flies were captured and identified, belonging to three subtribes, nine genera, and 14 species (13 of which were able to be determined), with a balanced sex ratio of 0.95 males per each female. *Lutzomyia longipalpis* was the most abundant species in the survey, accounting for 62.61% of the total catches; however, this species was restricted to El Progreso and Huehuetenango, with Huehuetenango having the highest capture percentage (55.54%). This vector was predominantly found outdoors, mostly in extra-domicile areas (62.29%). The male/female ratio for this species was 1.94. This study, and the entomological data we present, can aid in enhancing vector control interventions in these northern departments, thereby decreasing the incidence of leishmaniosis in humans.

Resumen—En Guatemala, tres millones de personas se encuentran en riesgo de contraer leishmaniosis cutánea, principalmente en las regiones del norte. A pesar de esta alarmante situación epidemiológica, se han realizado pocos estudios faunísticos sobre los flebotomos en este país, el más poblado de América Central. Se llevó a cabo un estudio entomológico de los flebotomos desde marzo hasta septiembre de 2018 en áreas rurales, montañosas y forestales de seis departamentos del norte de Guatemala con transmisión activa de leishmaniosis en seres humanos: Petén, Huehuetenango, Quiché, Alta Verapaz, Izabal y El Progreso. Se colocaron trampas de luz tipo mini-CDC dentro y alrededor de viviendas con casos recientes de leishmaniosis en niños menores de 10 años de edad. Se capturaron e identificaron un total de 2,605 ejemplares de flebotomos, que pertenecieron a tres subtribus, nueve géneros y 14 especies (13 de las cuales

pudieron determinarse), con una proporción de sexos equilibrada de 0.95 machos por cada hembra. La especie más abundante en el estudio fue *Lutzomyia longipalpis*, que representó el 62.61% del total de capturas; sin embargo, esta especie se limitó a El Progreso y Huehuetenango, siendo Huehuetenango el lugar con el porcentaje de capturas más elevado (55.54%). Este vector se encontró predominantemente en exteriores, sobre todo en el extradomicilio (62.29%). La proporción de machos/hembras para esta especie fue de 1.94. Este estudio y los datos entomológicos que presentamos pueden contribuir a mejorar las intervenciones de control de vectores en estos departamentos del norte, reduciendo así la incidencia de leishmaniosis en seres humanos.

Subfamily Phlebotominae (Diptera: Psychodidae) includes about 532 extant, described species in the New World (Galati 2021). It is a group in which females are hematophagous, with certain species involved in the transmission of pathogens to vertebrates (Maroli et al. 2013). The most significant is their role as vectors of *Leishmania* spp. among mammals. However, sand flies are also natural vectors of arboviruses (*Phlebovirus*, *Vesiculovirus*, and *Orbivirus*) worldwide (Ayhan and Charrel 2017), and *Bartonella bacilliformis* in South America (Sanchez Clemente et al. 2012).

Protozoan species of *Leishmania* (Kinetoplastida: Trypanosomatidae) are the causal agents of leishmaniases in wild vertebrates and constitute a group of zooanthroponotic diseases with a diverse spectrum of clinical manifestations. The characteristics of these diseases vary greatly, but they are often divided into three distinct clinical syndromes, namely visceral leishmaniosis (VL), a potentially life-threatening condition if left untreated, cutaneous leishmaniosis (CL), and mucosal leishmaniosis (ML) (Murray et al. 2005). Globally, leishmaniases are among the top 10 neglected tropical diseases, with more than 12 million infected people, 0.9 to 1.6 million new cases each year, between 20,000 and 30,000 deaths, and 350 million people at risk of infection. In the Americas, an average of 56,000 cases of CL and ML, and 3,800 cases of VL, are recorded annually, with an average case fatality rate of 7% (PAHO 2023a). In Guatemala, the most populous country in Central America, three million people are estimated to be at risk of contracting CL, primarily in the northern regions (Fundación Probitas 2023).

Few taxonomic or faunistic studies of phlebotomine sand flies have been conducted in Guatemala. Fairchild and Hertig (1948, 1950, 1952, 1956) and Young (1977) reported some species, and more recently, De León (1971) and Porter and Young (1986, 1999) described three additional species; however, one species of genus *Dampfomyia* remains to be formally described (Young and Duncan 1994). Rowton et al. (1991) conducted the most comprehensive study involving systematic collections. These contributions identify 35 species of phlebotomine sand flies in Guatemala (Shimabukuro et al. 2017; Galati 2018, 2021). Among these, five species have been linked to the transmission of human leishmaniosis in the country: *Lutzomyia longipalpis* (Lutz and Neiva 1912); *Nyssomyia ylephiletor* (Fairchild and Hertig 1952); *Ny. trapidoi* (Fairchild and Hertig 1952); *Psychodopygus panamensis* (Shannon 1926); and *Pintomyia ovallesi* (Ortiz 1952) (Rowton et al. 1991).

Over the last decades, ecological and climatic changes caused by anthropogenic activities such as irrigation, dam construction, deforestation, and urbanization have resulted in drastic changes in vector distribution and population densities (Maroli et al. 2013; Alarcón-Elbal 2018). Despite this alarming situation, relatively little is known about these vectors in the country, and there is a scarcity of recent entomological studies focusing on them. In addition, these diseases involve domestic dogs and wild canines (foxes, jackals, and wolves), as well as other undetermined vertebrate hosts that serve as reservoir hosts and increase the likelihood of disease transmission to humans (WHO 2023).

This study aimed to determine the species composition and relative abundance of sand flies in six Guatemalan departments with active transmission of human leishmaniases. The identification of such entomological information facilitates the development of specific vector control interventions in the region and, as a result, the reduction of disease burden.

Materials and Methods

Study area

In 2017, the Health Management Information System reported 775 cases of CL and two cases of VL in Guatemala, with the majority occurring in the northern departments of Petén, Huehuetenango, Quiché, Alta Verapaz, and Izabal (PAHO 2019, 2023b). For this

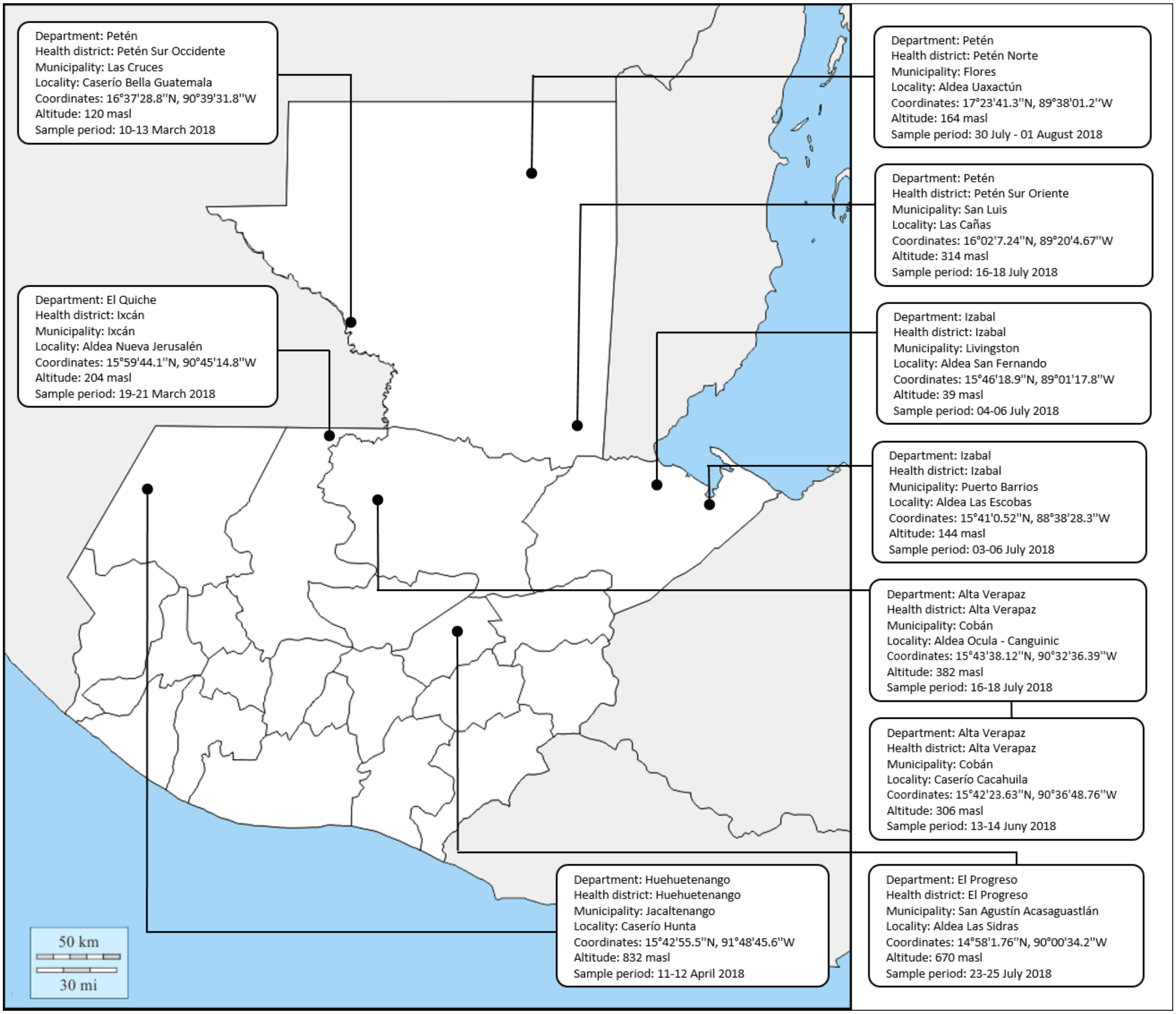

FIG. 1. Spatial representation of the sampling points of phlebotomine sand flies in Guatemala in 2018, including department, health district, municipality, locality, coordinates, altitude, and sample period information.

reason, an entomological survey of phlebotomine sand flies was conducted from March to September, 2018 in rural, mountainous, and forested areas of these departments; however, El Progreso was also included for reporting cases of VL. A single location was sampled in each department, with the exception of Izabal and Alta Verapaz, which had two sampling locations each. Lastly, catches in Petén, which is the largest department, were detailed for this study according to its three health areas: Petén Sur Occidental, Petén Sur Oriental, and Petén Norte (Fig. 1).

These departments are situated in coastal plains and lowlands with a tropical climate according to the Köppen-Geiger classification, with an average annual temperature of approximately 27° C. This region of the country is extremely rainy, with the heaviest rainfall occurring between June and October, and an average annual rainfall between 1,559.1 and 1,718.2 mm (INSVMH 2023).

Sand fly collections and identification

Three houses were selected at each sampling location. The criteria for selecting the houses were recent cases of leishmaniosis in children under 10 years of age. Three Centers for Disease Control and Prevention (CDC) miniature light traps (John W. Hock Company, Florida, U.S.A.) were used to capture sand flies at each house. During three consecutive nights, traps were set 1.5 m above the ground in intra-domicile (the living room), peri-domicile (the yard), and extra-domicile areas (25 m from the house). Traps were deployed at 18:00, and collected at 06:00 the following morning. Sand flies were collected and stored in labelled tubes with 70% alcohol before being mounted on glass slides using Canada balsam for the males, and Berlese's fluid for the females. Afterwards, the males were identified by examining the external genitalia, while the females were identified by examining the pharynx and spermathecae using the appropriate taxonomic keys (Young and Duncan 1994; Galati 2018). The phlebotomine specimens are deposited in Laboratorio de Referencia Taxonómica e Identificación de Entomología Médica, Guatemala City, Guatemala.

RESULTS

In this study, a total of 2,605 specimens of sand flies were captured and identified, belonging to three subtribes, nine genera, 13 defined species, and one undetermined species of the group Delpozoi, with a balanced sex ratio (number of males/number of females = 0.95).

Below is a list of the taxa collected for this study, along with brief comments on the taxonomic history, material examined, distribution, bionomics, and medical relevance.

SERGENTOMYIINA Artemiev 1991
Genus *Micropygomyia* Barretto 1962
Subgenus *Micropygomyia* (*Micropygomyia*) s. str. Barretto 1962
Series Cayennensis

- *Micropygomyia (Micropygomyia) cayennensis maciasi* (Fairchild and Hertig 1948)

cayennensis maciasi Fairchild and Hertig 1948: 466 (as subspecies of *Phlebotomus cayennensis*).

Type locality: Mexico, Guerrero, Zumpango; Guatemala, Escuintla.

Taxonomic history: See Ibáñez-Bernal and Durán-Luz (2022).

Material examined: Guatemala: Department of El Progreso, Municipality of San Agustín Acasaguastlán, Aldea Las Sidras, 23–25 July 2018, 1 ♀; Department of Petén (Sur Occidental), Municipality of Las Cruces, Caserío Bella Guatemala, 10–13 March 2018, 1 ♂; Department of Petén (Sur Oriental), Municipality of San Luis, Las Cañas, 16–18 July 2018, 7 ♂♂; Department of Quiché, Municipality of Ixcán, Aldea Nueva Jerusalén, 19–21 March 2018, 6 ♀♀.

The males could not be assigned to a subspecies but were considered *Mi. cayennensis maciasi* due to their association with the females.

Distribution: Belize, Guatemala, and Mexico (Martins et al. 1978; Young and Duncan 1994; Shimabukuro et al. 2017; Galati 2018, 2021; Ibáñez-Bernal and Durán-Luz 2022). In Guatemala, this species was previously documented in the Municipality of San José, Escuintla Department (Martins et al. 1978).

Bionomics and medical relevance: Females of *Micropygomyia* species are not anthropophilic, but it is known that some species feed on lizards (Young and Duncan 1994); therefore, it is likely that *Mi. (Mic.) cayennensis maciasi* feeds on reptiles (Ibáñez-Bernal and Rebollar-Téllez 2023). There is no information about its vector competence.

LUTZOMYIINA Abonnenc and Léger 1976
Genus *Lutzomyia* França 1924
Subgenus *Lutzomyia* (*Lutzomyia*) s. str.

- *Lutzomyia (Lutzomyia) longipalpis* (Lutz and Neiva 1912)

longipalpis Lutz and Neiva 1912: 89 (as *Phlebotomus*).

Type locality: Brazil, locality not specified.

Taxonomic history: See Ibáñez-Bernal and Durán-Luz (2022).

Material examined: Department of El Progreso, Municipality of San Agustín Acasaguastlán, Aldea Las Sidras, 23–25 July 2018, 97 ♀♀, 133 ♂♂; Department of Huehuetenango, Municipality of Jacaltenango, Caserío Hunta, 11–12 April 2018, 458 ♀♀, 943 ♂♂.

Distribution: Argentina, Bolivia, Brazil, Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Paraguay, Uruguay, and Venezuela (Williams 1991; Shimabukuro et al. 2017; Galati 2018, 2021; Ibáñez-Bernal and Durán-Luz 2022). In Guatemala, this species was previously recorded in El Progreso and Zacapa (?) departments (Martins et al. 1978).

Bionomics and medical relevance: *Lutzomyia (Lut.) longipalpis* feeds on chickens and other birds, cows, dogs, goats, hamsters, horses, donkeys, oxen, pigs, and humans (De Buen et al. 1966; Morrison et al.

1993a; Ogusuku et al. 1994; Alfonso et al. 2012; Mejía et al. 2018). It is considered the primary vector of *Leishmania infantum* (Killick-Kendrick 1990; Maroli et al. 2013) and *L. amazonensis* in Brazil (Young and Duncan 1994). Bates (2007) mentioned this species as a vector of *L. infantum* in humans, and considered domestic dogs and foxes as important reservoirs in Central and South America.

Subgenus *Lutzomyia* (*Tricholateralis*) Galati 1995

- *Lutzomyia (Tricholateralis) cruciata* (Coquillett 1907)

cruciata Coquillett 1907: 102 (as *Phlebotomus cruciatus*).

Type locality: Guatemala, Alta Verapaz, Trece Aguas, Cacao.

Taxonomic history: See Ibáñez-Bernal and Durán-Luz (2022).

Material examined: Guatemala: Department of Huehuetenango, Municipality of Jacaltenango, Caserío Hunta, 11–12 April 2018, 4 ♀♀, 4 ♂♂; Department of Petén (Norte), Municipality Flores, Aldea Uaxactún, 30 July–1 August 2018, 6 ♀♀; Department of Petén (Sur Oriental), Municipality of San Luis, Las Cañas, 16–18 July 2018, 4 ♀♀; Department of Quiché, Municipality of Ixcán, Aldea Nueva Jerusalén, 19–21 March 2018, 11 ♀♀; Department of Alta Verapaz, Municipality of Cobán, Caserío Cacahuila, 13–14 June 2018, 1 ♀; Department of Alta Verapaz, Municipality of Cobán, Aldea Ocula–Canguinic, 16–18 July 2018, 2 ♀♀; Department of Izabal, Municipality of Livingston, Aldea San Fernando, 4–6 July 2018, 2 ♀♀; Department of Izabal, Municipality of Puerto Barrios, Aldea Las Escobas, 3–6 July 2018, 5 ♀♀.

Distribution: Belize, Brazil, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, and U.S.A. (Shimabukuro et al. 2017; Galati 2018, 2021; Ibáñez-Bernal and Durán-Luz 2022). In Guatemala, this species was documented in Trece Aguas, Alta Verapaz (the type locality), Tikal, Petén (Rowton et al. 1991), and the departments of Escuintla, Sololá, San Miguel, San Vicente, and Sonsonate (Young and Perkins 1984).

Bionomics and medical relevance: This species is anthropophilic (Young and Perkins 1984; Young and Duncan 1994). In Honduras, Mejía et al. (2018) found that *Lu. cruciata* feeds on human and dog blood, and in Mexico, De Buen et al. (1966) found that it feeds on hamster blood. It has been considered an important vector of *L. braziliensis*, *L. panamensis*, and *L. mexicana* (Pech-May et al. 2010; Maroli et al. 2013).

Genus *Pintomyia* Costa Lima 1932
Subgenus *Pintomyia* (*Pifanomyia*) Ortiz and Scorza 1963
Series Evansi

- *Pintomyia (Pifanomyia) evansi* (Nuñez-Tovar 1924)

evansi Nuñez-Tovar 1924: 44 (as *Phlebotomus*).

Type locality: Venezuela, Carabobo, Mariara.

Taxonomic history: See Ibáñez-Bernal and Durán-Luz (2022).

Material examined: Guatemala: Department of El Progreso, Municipality of San Agustín Acasaguastlán, Aldea Las Sidras, 23–25 July 2018, 395 ♀♀, 87 ♂♂.

Distribution: Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Peru, and Venezuela (Shimabukuro et al. 2017; Galati 2018, 2021; Ibáñez-Bernal and Durán-Luz 2022). In Guatemala, this species was recorded in the Escuintla Department (Fairchild and Hertig 1959).

Bionomics and medical relevance: Females of this species feed on human blood and are considered vectors of *L. infantum* (Osorno-Mesa et al. 1972; Young 1979; Young and Duncan 1994; Maroli et al. 2013). *Pintomyia evansi* has been found to feed on the blood of cows, horses, pigs, chickens, mice, and humans in Colombia (Paternina et al. 2016), and dogs, pigs, and chickens in Honduras (Mejía et al. 2018). It was discovered alongside *Lu. longipalpis* (considered to be the primary vector) and *Lu. cruciata* in an endemic focus of VL in Chiapas, Mexico (Ibáñez-Bernal e al. 2004; Ibáñez-Bernal and Rebollar-Téllez 2023).

- *Pintomyia (Pifanomyia) ovallesi* (Ortiz 1952)

ovallesi Ortiz 1952: 155 (as *Phlebotomus*).

Type locality: Venezuela, Lara, Duaca.

Taxonomic history: See Ibáñez-Bernal and Durán-Luz (2022).

Material examined: Guatemala: Department of Petén (Norte), Municipality of Flores, Aldea Uaxactún, 30 July–1 August 2018, 95 ♀♀; Department of El Progreso, Municipality of San Agustín Acasaguastlán, Aldea Las Sidras, 23–25 July 2018, 1 ♀; Department of Petén (Sur Oriental), Municipality of San Luis, Las Cañas, 16–18 July 2018, 2 ♀♀, 3 ♂♂.

Distribution: Belize, Colombia, Costa Rica, Guatemala, Honduras, Mexico, Nicaragua, Panama, Trinidad and Tobago, and Venezuela (Rowton et al. 1991; Young and Duncan 1994; Shimabukuru et al. 2017; Galati 2018, 2021; Ibáñez-Bernal and Durán-Luz 2022). In Guatemala, this species was recorded in the Department of Petén, Municipality of Flores, Tikal (Rowton et al. 1991).

Bionomics and medical relevance: This species feeds on a wide range of vertebrates, including humans. The transmission of *L. braziliensis* and *L. mexicana* to humans is attributed to this species (De Buen et al. 1966; Osorno-Mesa et al. 1972; Young 1979; Feliciangeli et al. 1988; Maroli et al. 2013). Pech-May et al. (2010) collected female specimens using a human-baited Shannon trap, whereas none were collected using a mouse-baited Disney trap (Ibáñez-Bernal and Rebollar-Téllez 2023).

Genus *Dampfomyia* Addis 1945
Subgenus *Dampfomyia* (*Coromyia*) Barretto 1962

- *Dampfomyia (Coromyia) deleoni* (Fairchild and Hertig 1947)

deleoni Fairchild and Hertig 1947: 622 (as *Phlebotomus*).

Type locality: Guatemala, Petén.

Taxonomic history: See Ibáñez-Bernal and Durán-Luz (2022).

Material examined: Guatemala: Department of Huehuetenango, Municipality of Jacaltenango, Caserío Hunta, 11–12 April 2018, 1 ♀, 2 ♂♂; Department of Petén (Sur Oriental), Municipality of San Luis, Las Cañas, 16–18 July 2018, 19 ♀♀, 7 ♂♂.

Distribution: Belize, Costa Rica, El Salvador, Guatemala, Honduras, and Mexico (Shimabukuro et al. 2017; Galati 2018, 2021; Ibáñez-Bernal and Durán-Luz 2022). In Guatemala, this species was recorded in the Department of Petén (the type locality), and Rowton et al. (1991) reported it in the Department of Petén, Municipality of Flores, Tikal.

Bionomics and medical relevance: Williams (1976) captured specimens of this species in caves in Belize. Porter et al. (1987) and Rowton et al. (1991) used human bait to capture female specimens. Rebollar-Téllez et al. (1996) collected specimens using funnel traps set over mammal burrows in Mexico, and Pech-May et al. (2010) collected them using a human-baited Shannon trap and a mouse-baited Disney trap. Its importance as a vector is unknown.

- *Dampfomyia (Coromyia) disneyi* (Williams 1987)

disneyi Williams 1987: 525 (as *Lutzomyia* (*Coromyia*)).

Type locality: Belize, Cayo District, San Antonio.

Taxonomic history: See Ibáñez-Bernal and Durán-Luz (2022).

Material examined: Guatemala: Department of Huehuetenango, Municipality of Jacaltenango, Caserío Hunta, 11–12 April 2018, 2 ♀♀; Department of Petén (Sur Oriental), Municipality of San Luis, Las Cañas, 16–18 July 2018; 1 ♂.

Distribution: Belize, Guatemala, and Mexico (Williams 1987; Ibáñez-Bernal et al. 2015; Shimabukuro et al. 2017; Galati 2018, 2021). According to Young and Duncan (1994), C.H. Porter recorded it in Guatemala, Petén Department, Municipality of Poptún, Coop. Tanhoc.

Bionomics and medical relevance: This species inhabits caves and is considered a potential vector of chiropteran trypanosomes (Young and Duncan 1994).

- *Dampfomyia* group *Delpozoi*, sp. indet.

Material examined: Guatemala: Department of Petén (Sur Oriental), Municipality of San Luis, Las Cañas, 16–18 July 2018, 5 ♀♀; Department of Alta Verapaz, Municipality of Cobán, Aldea Ocula–Canguinic, 16–18 July 2018, 1 ♀.

Distribution: Three species of this group are known in southern Mexico, Belize, and Guatemala: *Dampfomyia inusitata* (Fairchild and Hertig 1961) from Mexico; *Da. delpozoi* from Belize, Guatemala, and Mexico; and an undescribed species, "de Suchitepequez" (Young and Duncan 1994). This species could not be determined with only females available.

Bionomics and medical relevance: There is no information regarding feeding habits or their importance as a vector.

Subgenus *Dampfomyia* (*Dampfomyia*) Addis 1945

- *Dampfomyia (Dampfomyia) atulapai* (De León 1971)

atulapai De León 1971: 187 (as *Phlebotomus*).

Type locality: Guatemala, Chiquimula, Atulapa River.

Taxonomic history: See Ibáñez-Bernal and Durán-Luz (2022).

Material examined: Guatemala: Department of Huehuetenango, Municipality of Jacaltenango, Caserío Hunta, 11–12 April 2018, 1 ♀, 1 ♂.

Distribution: El Salvador, Guatemala, and Mexico (Young and Duncan 1994, Shimabukuro et al. 2017, Galati 2018, Galati 2021, Ibáñez-Bernal and Durán-Luz 2022).

Bionomics and medical relevance: The feeding habits are unknown.

Genus *Trichopygomyia* Barretto 1962

- *Trichopygomyia triramula* (Fairchild and Hertig 1952)

triramula Fairchild & Hertig, 1952: 517, 525 (as *Phlebotomus triramulus*).

Type locality: Panama, Colón, Medio.

Taxonomic history: See Ibáñez-Bernal and Durán-Luz (2022).

Material examined: Guatemala: Department of Quiché, Municipality of Ixcán, Aldea Nueva Jerusalén, 19–21 March 2018, 108 ♀♀, 73 ♂♂.

Distribution: Belize, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, and Panama (Shimabukuro et al. 2017; Galati 2018, 2021; Ibáñez-Bernal and Durán-Luz 2022).

Bionomics and medical relevance: The feeding habits are unknown.

PSYCHODOPYGINA Galati 1995

Genus *Psathyromyia* Barretto 1962

Subgenus *Psathyromyia* Barretto, sensu stricto

- *Psathyromyia (Psathyromyia) undulata* (Fairchild and Hertig 1950)

undulata Fairchild and Hertig 1950: 524 (as *Phlebotomus undulatus*).

Type locality: Guatemala, between Escuintla and San José.

Taxonomic history: See Ibáñez-Bernal and Durán-Luz (2022).

Material examined: Guatemala: Department of Izabal, Municipality of Puerto Barrios, Aldea Las Escobas, 3–6 July 2018, 1 ♀.

Distribution: Belize, Bolivia, Colombia, Costa Rica, Ecuador, El Salvador, French Guiana, Guatemala, Honduras, Mexico, and Panama (Shimabukuro et al. 2017; Galati 2018, 2021; Ibáñez-Bernal and Durán-Luz 2022).

Bionomics and medical relevance: It is not anthropophagous. Tesh et al. (1971, 1972) observed that this species feeds on rodents, marsupials, and carnivorous mammals in Panama.

Genus *Bichromomyia* Artemiev 1991

- *Bichromomyia olmeca olmeca* (Vargas and Díaz-Nájera 1959)

olmeca Vargas and Díaz-Nájera 1959: 147 (as *Phlebotomus olmecus* ♂, the ♀ corresponds to *Bi. ylephiletor*).

Type locality: Mexico, Tabasco, Teapa.

Taxonomic history: See Ibáñez-Bernal and Durán-Luz (2022).

Material examined: Guatemala: Department of Petén (Sur Oriental), Municipality of San Luis, Las Cañas, 16–18 July 2018,1 ♀; Department of Izabal, Municipality of Puerto Barrios, Aldea Las Escobas, 3–6 July 2018, 1 ♂.

Distribution: Belize, Costa Rica, Guatemala, Honduras, Mexico, and Nicaragua (Shimabukuro et al. 2017; Galati 2018, 2021; Ibáñez-Bernal and Durán-Luz 2022).

Bionomics and medical relevance: Females of this species are known to feed on the blood of rodents and humans (Biagi et al. 1965; De Buen et al. 1966; Disney 1968) and are capable of transmitting *L. mexicana* to humans (Killick-Kendrick 1990; Young and Duncan 1994; Maroli et al. 2013). In Mexico, Pech-May et al. (2010) collected specimens of this species using a human-baited Shannon trap and a rodent-baited Disney trap. Sánchez-García et al. (2010) collected *Bi. olmeca olmeca* specimens using the same traps and discovered a natural infection with *L. mexicana* in specimens collected using both traps.

Genus *Psychodopygus* Mangabeira 1941

Series Panamensis

- *Psychodopygus panamensis* (Shannon 1926)

panamensis Shannon 1926: 192 (as *Phlebotomus*).

Type locality: Panama, Canal Zone, Cano Saddle.

Taxonomic history: See Ibáñez-Bernal and Durán-Luz (2022).

Material examined: Guatemala: Department of El Progreso, Municipality of San Agustín Acasaguastlán, Aldea Las Sidras, 23–25 July 2018, 1 ♀; Department of Petén (Norte), Municipality of Flores, Aldea Uaxactún, 30 July–1 August 2018, 43 ♀♀, 2 ♂♂; Department of Izabal, Municipality of Puerto Barrios, Aldea Las Escobas, 3–6 July 2018, 2 ♀♀, 2 ♂♂; Department of Petén (Sur Oriental), Municipality of San Luis, Las Cañas, 16–18 July 2018, 1 ♀.

Distribution: Belize, Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Guatemala, Honduras, Mexico, Nicaragua, Panama, Peru, Suriname, and Venezuela (Shimabukuro et al. 2017; Galati 2018, 2021; Ibáñez-Bernal and Durán-Luz 2022).

Bionomics and medical relevance: This is a well-known anthropophagous species (Porter and De Foliart 1981; Young and Duncan 1994; Pech-May et al. 2010; Anaguano et al. 2015) that also feeds on domestic animals (De Buen et al. 1966). Pech-May et al. (2010) collected a few specimens using a rodent-baited Disney trap. Strangways-Dixon et al. (1966) succeeded in the experimental transmission of *L. mexicana* to hamsters. It is considered a primary vector of *L. colombiensis*, *L. braziliensis*, *L. mexicana*, and *L. panamensis* that affect humans (Christensen et al. 1983; Young and Duncan 1994; Maroli et al. 2013). Paternina et al. (2016) discovered horse, cow, rodent, and human blood in the digestive tracts of female specimens.

Genus *Nyssomyia* Barretto 1962

- *Nyssomyia ylephiletor* (Fairchild and Hertig 1952) *ylephiletor* Fairchild and Hertig 1952: 520 (as *Phlebotomus*).

Type locality: Panama, Bocas del Toro, Almirante.

Taxonomic history: See Ibáñez-Bernal and Durán-Luz (2022).

Material examined: Guatemala: Department of Huehuetenango, Municipality of Jacaltenango, Caserío Hunta, 11–12 April 2018, 31 ♀♀; Department of Quiché, Municipality of Ixcán, Aldea Nueva Jerusalén, 19–21 March 2018, 2 ♀♀; Department of Petén (Sur Oriental), Municipality of San Luis, Las Cañas, 16–18 July 2018, 19 ♀♀, 2 ♂♂; Department of Izabal, Municipality of Puerto Barrios, Aldea Las Escobas, 3–6 July 2018, 7 ♀♀; Department of Alta Verapaz, Municipality of Cobán, Aldea Ocula–Canguinic, 16–18 July 2018, 1 ♀.

Distribution: Belize, Colombia, Costa Rica, Ecuador, Guatemala, Honduras, Mexico, Nicaragua, and Panama (Shimabukuro et al. 2017; Galati 2018, 2021; Ibáñez-Bernal and Durán-Luz 2022).

Bionomics and medical relevance: Tesh et al. (1971) reported that this species is anthropophilic but feeds on the blood of various mammals. Pech-May et al. (2010) collected specimens using a human-baited Shannon trap, whereas none were collected using a rodent-baited Disney trap. It is considered a vector of *L. braziliensis*, *L. mexicana*, and *L. panamensis* (Porter et al. 1987; Young and Duncan 1994; Maroli et al. 2013).

Discussion

In addition to their bites, which can cause allergic reactions, phlebotomine sand flies are of great medical and veterinary interest due to their central role in the epidemiological cycle of certain diseases. Sand-fly-borne diseases, especially the various forms of leishmaniases and arboviruses, continue to be important public health issues in many countries of the world, even in temperate regions (Alarcón-Elbal and González 2022).

In Guatemala, leishmaniosis is currently endemic in five departments: Petén and Alta Verapaz (located in northern Guatemala) have the highest number of reported cases, followed by Izabal (northeast), Quiché, and Huehuetenango (northwest). Cutaneous leishmaniosis, the most prevalent clinical form in the country and commonly known as 'la chiclera,' is caused by *L. panamensis*, *L. mexicana*, and *L. braziliensis*. It is reported in the northern departments, especially in the forested areas of Petén and Alta Verapaz. Visceral leishmaniosis is caused by *L. infantum* and has only been reported in the semi-arid valleys and foothills of Guatemala in the Department of El Progreso (east-central), as well as in Huehuetenango (CES 2022). Although no cases of ML have been recorded, the emergence of cases cannot be discarded.

Taking into account the sampling effort (number of sampling sites) by department, Huehuetenango had the highest percentage of catches (59.13%), followed by El Progreso (29.22%), Quiché (8.17%), and with anecdotal percentages for Petén (2.97%), Izabal (0.41%), and Alta Verapaz (0.10%) (Fig. 2A). Huehuetenango was also the department where the highest number of taxa were found (6/14), followed by Petén Sur Oriental, Petén Sur Occidental, Izabal, and El Progreso (5/14 each). Due to the fact that each location was sampled for three consecutive nights (which is one of the limitations of the study), no phenology could be determined. In fact, the absence of certain species at a given location may be the result of multiple factors, such as unsuitable environmental conditions at the time of sampling (the sampling period between March and September could also result in seasonal biases), and even the site selection of the trap at the micro-scale level.

To date, Guatemala has a total of 35 known species of sand flies (Shimabukuro et al. 2017), but nearly

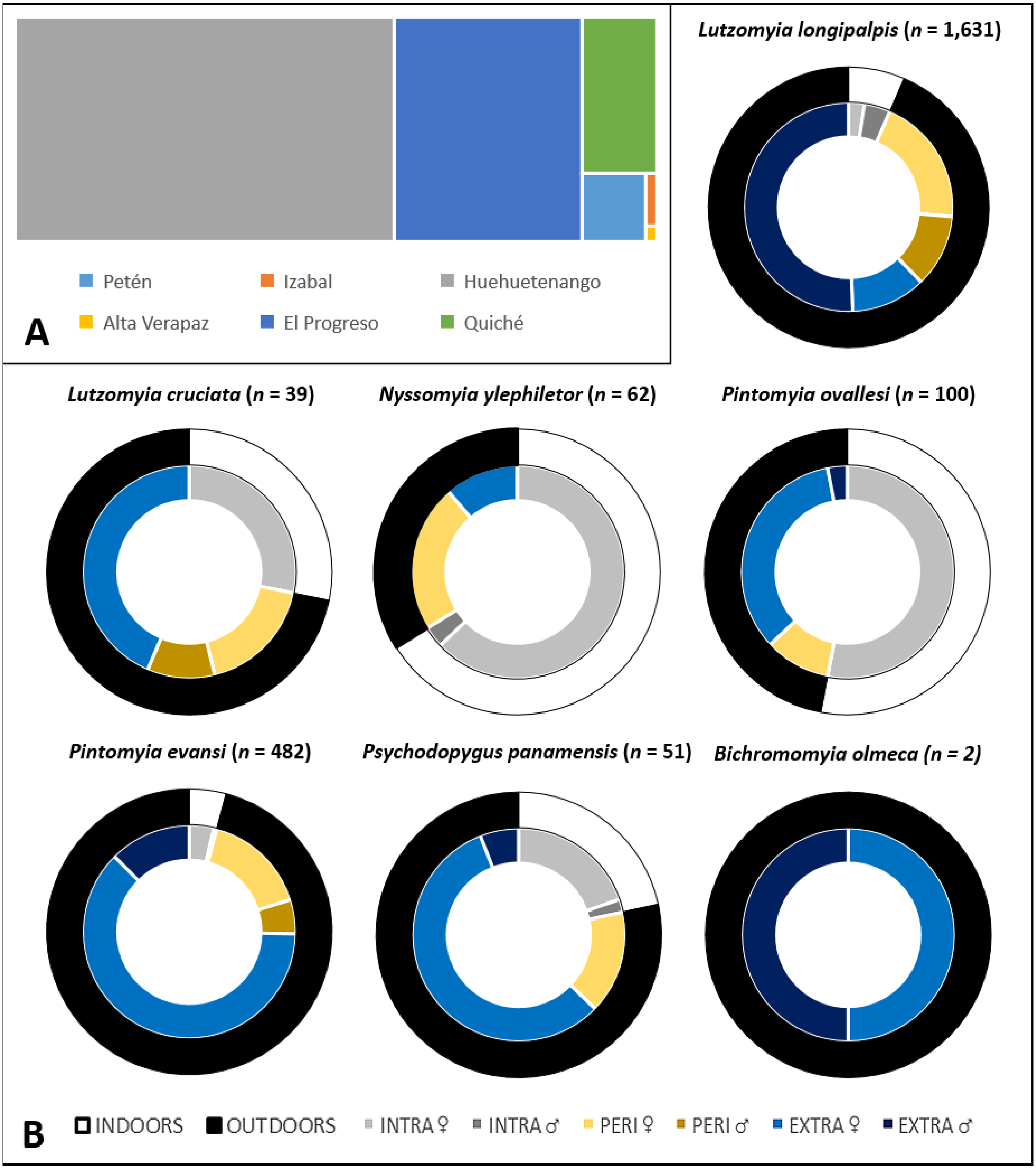

FIG. 2. A. Graphical representation of mean abundance of total sand fly catches by department; B. Graphical representation of the mean abundance of phlebotomine sand fly specimens by trap location indoors (intra-domicile) and outdoors (peri- and extra-domicile) for each of the species of vector interest captured in the northern departments of Guatemala, 2018.

all records are sporadic and obtained from a single or a few collections, making it difficult to determine the distribution of the species in the country. Consequently, the distribution and species richness of these dipterans in the country may be underestimated. Faunal studies, like the present one, are essential for identifying the distribution of species, particularly those involved in the transmission of *Leishmania* spp. to humans, which enables the identification of areas or zones with a greater risk of transmission.

Of the 14 taxa identified in our study, four species have been reported as vectors of leishmaniosis in Guatemala (*Lu. longipalpis*, *Ny. ylephiletor*, *Pi. ovallesi*, and *Ps. panamensis*) (Rowton et al. 1991), and three other species have been reported as vectors of the disease in other countries of the Americas (*Bi. olmeca olmeca*, *Lu. cruciata*, and *Pi. evansi*) (Maroli et al. 2013). The main vector in the New World, *Lu. longipalpis*, was only captured in the departments of El Progreso and Huehuetenango, but accounted for 62.61% of the total (*n* = 1,631). Both *Lu. cruciata* and *Ny. ylephiletor* were found in five departments, making them the most widely distributed species. The high prevalence of *Lu. longipalpis* in leishmaniosis foci has been reported in other countries such as Bolivia, Costa Rica, and Brazil (Zeledon et al. 1984; Le Pont and Desjeux 1985; Ximenes et al. 1999). More recently, Flórez et al. (2006) reported that this sand fly was the predominant species in a Colombian suburb where VL was prevalent, accounting for 99.5% of their captures. The second most abundant species caught was *Pi. evansi* (*n* = 482, 18.5%), a sand fly that plays an important role in the transmission of this disease in some areas of South America (Travi et al. 1996). This vector is followed by six species with a relative abundance of less than 7%: *Tr. triramula* (*n* = 181, 6.94%); *Pi. ovallesi* (*n* = 101, 3.87%); *Ny. ylephiletor* (*n* = 62, 2.32%); *Ps. panamensis* (*n* = 59, 1.95%); *Lu. cruciata* (*n* = 39, 1.49%); and *Da. deleoni* (*n* = 29, 1.11%). Among these species, *Pi. ovallesi*, *Ny. ylephiletor*, and *Ps. panamensis* are confirmed as vectors of human leishmaniosis in Guatemala (Rowton et al. 1991). Finally, six species had a relative abundance of less than 1%, and their presence in this study area was, therefore, sporadic: *Mi. cayannensi maciasi* (*n* = 15, 0.57%); *Dampfomyia* group Delpozoi (*n* = 6, 0.23%); *Da. disneyi* (*n* = 3, 0.11%); *Da. atulapai* (*n* = 2, 0.07%); *Bi. olmeca olmeca* (*n* = 2, 0.07%); and *Pa. undulata* (*n* = 1, 0.04%) (Table 1).

Considering the leishmaniosis vectors in the country and according to our results, the most ubiquitous species was *Lu. cruciata*, which appeared in five departments, although the most abundantly captured was *Lu. longipalpis* (Table 1). Sand flies of this species are primarily found outdoors in large numbers in animal pens, particularly chicken sheds, and in much smaller numbers inside houses (Quinnell and Dye 1994). Although the role of chickens in the epidemiology of leishmaniosis is unclear, the presence of these birds and other domestic animals has been reported as a risk factor for human infection (Belo et al. 2013). Other risk factors include poor housing conditions and household sanitation deficits, malnutrition and immunological status, and an increase in deforestation (Barata et al. 2011). In our study, *Lu. longipalpis* was predominantly found outdoors, primarily in extra-domicile areas (11.65% females, 50.64% males), followed by peri-domicile areas (19.93% females, 11.28% males); indoor captures did not exceed 7% of the total (2.45% females, 4.05% males). These percentages were calculated based on the total number of individuals of this species captured in the two previously mentioned departments. The literature indicates that this species is most frequently captured outdoors, possibly due to the presence of domestic animals such as dogs (Quinnell and Dye 1994; Barata et al. 2011). In a study similar to ours conducted in Minas Gerais, Brazil, *Lu. longipalpis* was the predominant species, accounting for 85.8% of the total specimens collected outdoors (Lana et al. 2021). However, it can occasionally be found in large numbers inside the dwellings, such as in Santander, Colombia, where the species was found in greater abundance indoors (69.28%) than outdoors (30.18%) (Flórez et al. 2006). This may be attributed to a lack of available animal hosts, but also to the fact that *Lu. longipalpis* s.l. is a complex of sibling species with genetically differentiated populations, with habits ranging from jungle to urban, and from anthropophilic to zoophilic (Souza et al. 2017). Detailed percentages for species of vector interest by household location are shown in Fig. 2B.

The specific sex ratio for *Lu. longipalpis* was 1.94, with the males outnumbering the females. Other authors also report this male-biased sex ratio; for example, in the Amazonian region of Brazil, the ratio of males-to-females captured with CDC light traps was 1.37 (Dye et

Table 1. Species composition, abundance, and density of phlebotomine sand flies shown by department in Guatemala, 2018. The density of phlebotomines (in parentheses) was expressed as the number of specimens of each species collected per trap/night. In addition, it was considered for the analysis that two locations were sampled in Izabal and Alta Verapaz.

	Petén Norte	Petén Sur Oriental	Petén Sur Occidental	Huehuetenango	Quiché	Alta Verapaz	Izabal	El Progreso	Total
Bichromomyia olmeca olmeca	0	1 (0.11)	0	0	0	0	1 (0.05)	0	2
Dampfomyia deleoni	0	26 (2.89)	0	3 (0.33)	0	0	0	0	29
Dampfomyia group *Delpozoi* sp. indet.	0	5 (0.55)	0	0	0	1 (0.05)	0	0	6
Dampfomyia disneyi	0	0	1 (0.11)	2 (0.22)	0	0	0	0	3
Dampfomyia atulapai	0	0	0	2 (0.22)	0	0	0	0	2
Lutzomyia longipalpis	0	0	0	1,401 (155.67)	0	0	0	230 (25.55)	1,631
Lutzomyia cruciata	6 (0.67)	4 (0.44)	0	8 (0.89)	11 (1.22)	3 (0.17)	7 (0.38)	0	39
Micropygomyia cayannensi maciasi	0	7 (0.68)	1 (0.11)	0	6 (0.67)	0	0	1 (0.11)	15
Nyssomyia ylephiletor	0	0	21 (2.33)	31 (3.44)	2 (0.22)	1 (0.05)	7 (0.38)	0	62
Pintomyia evansi	0	0	0	0	0	0	0	482 (53.55)	482
Pintomyia ovallesi	95 (10.55)	0	5 (0.55)	0	0	0	0	1 (0.11)	101
Psathyromyia undulata	0	0	0	0	0	0	1 (0.05)	0	1
Psychodopygus panamensis	45 (5.00)	0	1 (0.11)	0	0	0	4 (0.22)	1 (0.11)	51
Trichopygomyia triramula	0	0	0	0	181 (20.11)	0	0	0	181
Total	146	43	29	1,447	200	5	20	715	**2,605**

al. 1991), while male *Lu. longipalpis* comprised 70.1% of CDC light trap collections in Colombia (Morrison et al. 1993b). This phenomenon can be explained by the fact that this sand fly species uses a sex-aggregation pheromone, which is released by males, to form aggregations of males and blood-meal-seeking females on or near different hosts (Kelly et al. 1997). In this sense, considering that the different areas studied are frequented by wild mammals such as sylvatic rodents, grey foxes, and fruit-eating bats that may serve as reservoirs of *Leishmania* spp. in Guatemala (Enríquez Sandoval 2019), active surveillance of the phlebotomine sand fly fauna is necessary to control the risk of transmission of this zoonosis, both to the local population and to those who visit or work in the localities studied.

There is a large number of specimens of vector species captured in the northern Guatemalan departments (n = 2,368, 90.90%), which represents a risk factor for the transmission of *Leishmania* spp. In addition, the emergence and re-emergence of leishmaniosis is strongly associated with environmental and anthropogenic changes. The reduction of forest cover as well as the proximity of human settlements to forested areas increase the risk of being bitten by infected females. In Guatemala, the loss of forest cover is particularly dramatic in Petén and other northern departments; on the other hand, poverty and lack of opportunities facilitate illegal settlement invasions in protected areas. In fact, deforestation in Petén has been shown to have changed the local micro-climate with reductions in humidity and increases in temperature of between 4 and 8° C in deforested areas compared to forested areas, increasing the risk of drought (Manoharan et al. 2009), and contributing to the emergence of vector-borne diseases such as leishmaniosis (Patz et al. 2000). Unfortunately, the control of these telmophagous dipterans is constrained by the inherent difficulties associated with their non-aquatic breeding sites, which are not susceptible to large-scale insecticidal treatment programmes (Alarcón-Elbal and González 2023). In the case of Guatemala, the lack of funds dedicated to the Vector-Borne Diseases Program and local socio-economic development explains the absence of progress in CL control (Mendizábal-Cabrera et al. 2021), as the country has experienced a significant increase in CL cases over the past few years (PAHO, 2019). Furthermore, in many countries in the Americas, research on medical and veterinary entomology is more focused on the study of mosquitoes (Culicidae), given the significant vectorial importance of these dipterans (Alarcón-Elbal et al. 2023). However, conducting studies on other groups such as sand flies, black flies (Simuliidae), or biting midges (Ceratopogonidae) also deserves attention and financial investment.

Finally, it is crucial for entomological and eco-epidemiological research to accurately identify the sand fly species that serve as vectors in a particular area and assess their ecology and behaviour (Pareyn et al. 2020). The morphological identification is time-consuming and labour-intensive, and requires a high level of expertise; however, this taxonomic approach remains fundamental, and it will be essential to find the right balance to integrate it with newer molecular methods and approaches, such as DNA barcoding (Alarcón-Elbal and Sandiford 2020; Alarcón-Elbal et al. 2021).

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