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Behavioral Aspects of *Lutzomyia longipalpis* (Diptera: Psychodidae) in Urban Area Endemic for Visceral Leishmaniasis

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ABSTRACT The study of some of the behavioral aspects of the main vector of *Leishmania infantum chagasi* Cunha & Chagas in the Americas, *Lutzomyia longipalpis* (Lutz & Neiva), such as dispersion, population size, and vector survival rates, is important for the elucidation of the mechanisms of visceral leishmaniasis transmission. These parameters were studied by means of capture-mark-release-recapture experiments in an urban area of Campo Grande municipality, an endemic area of visceral leishmaniasis, situated in Mato Grosso do Sul state, Brazil. Six capture-mark-release-recapture experiments were undertaken between November 2009 and November 2010 and once in January 2012 with a view to assessing the population size and survival rate of *Lu. longipalpis*. The insects were released in a peridomicile surrounded by 13 residences. The recaptures were undertaken with automatic light traps for four consecutive weeks after release in the surrounding area. In total, 3,354 sand flies were captured, marked, and released. The overall recapture rate during the capture-mark-release-recapture experiments was 4.23%, of which 92.45% were recaptured at the release site, indicating limited dispersal. The greatest distance recorded from the release site was 165 m for males and 241 m for females. The male daily survival rate, calculated on the basis of regressions from the numbers of marked recaptured insects during the 15 successive days after release was 0.897. The estimated male population size measured by the Lincoln Index was 10,947.127. Though *Lu. longipalpis* presented a limited dispersion the physical barriers typical of urban environments did not prevent the sand flies from flying long distances.

KEY WORDS *Lutzomyia longipalpis*, sand fly, mark-release-recapture, dispersal, survival

The dispersion and survival period of vectors are important aspects to the dissemination of diseases. However, there are few studies on this issue in forest and urban environments and little is known regarding the behavioral habits of the sand fly *Lutzomyia longipalpis* Lutz & Neiva (Brazil and Brazil 2003).

As one of the most important infectious diseases in the world, visceral leishmaniasis (VL) has broad geographic distribution and is a serious public health problem in Brazil, with records of notifications in all regions of the country (Werneck 2010). The high and growing incidence of this disease may be explained by environmental changes stemming from human activities, which have been altering the epidemiological profile in natural enzootic zones and peri-urban areas in which transmission involves domestic reservoirs (Deane and Grimaldi 1985, Shaw 2002).

Entomologic studies that analyze the behavior of insect vectors should consider issues inherent to the vector itself as well as the specific environmental characteristics of each region, such as the degree of urbanization, the presence of woodlands or remaining forest fragments, variations in climate, and spatial-temporal variations in the incidence of the illness studied (Medronho 1995).

Studies on the dispersion and behavioral patterns of sand flies were first carried out in the Old World (Quate 1964, Foster 1972, Killick–Kendrick et al. 1984), followed by studies conducted in the Americas (Chaniotis 1974, Alexander 1987, Alexander and Young 1992, Morrisson et al. 1993). The few publications on the longevity of sand flies in nature report 8 d for *Lu. longipalpis* (Morrison et al. 1993) and 14 d for *Nyssomyia neivai* Pinto (Casanova et al. 2005).

Little is known regarding the behavioral aspects of the main vector for *Leishmania infantum chagasi* Cunha & Chagas in the Americas (*Lu. longipalpis*) or the dynamics of VL transmission in the urban setting. Thus, investigations are needed to address these is-

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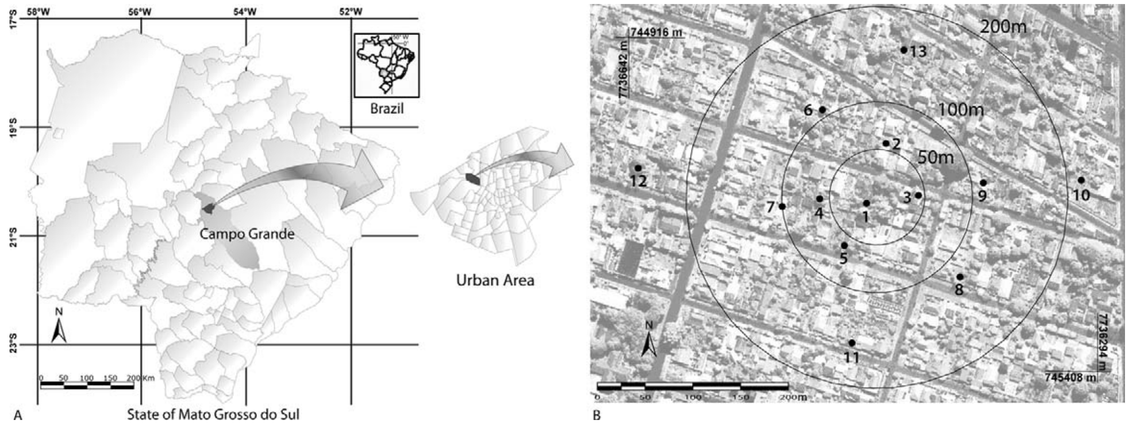

Fig. 1. Study area. (A) Municipal district of Campo Grande, State of Mato Grosso do Sul, Brazil. (B) 50, 100, and 200 m buffers and spatial distribution of recapture sites on IKONOS-2 image (panchromatic band).

sues, especially in endemic areas. The aim of the current study was to identify behavioral aspects of *Lu. longipalpis* through an analysis of population dispersion and longevity in nature.

Materials and Methods

Study Area. This study was carried out in an urban area endemic for VL in the municipality of Campo Grande (20° 26′34″ S, 54° 38′47″ W), which has a total area of 8,118.4 km^2 and is located in the central portion of the state of Mato Grosso do Sul, Brazil (Fig. 1A). The city is situated in the area belonging to the neotropical phytogeographic area known as the *Cerrado* (savanna). In the Köppen classification system, the climate of Campo Grande is wet tropical savanna, characterized by irregular rainfall distribution, with a well-defined dry season during the coldest months of the year and a rainy season during the summer months (Rohli and Veja 2008). According to estimates by the Brazilian Institute of Geography and Statistics, the urban population consisted of 766,461 inhabitants in 2010, corresponding to 98.7% of total (Instituto Brasileiro de Geografia e Estatística [IBGE] 2010).

The neighborhood of Santo Antonio is located in the western portion of Campo Grande and was selected for study. This choice was based on two criteria: 1) reports of human and canine cases in the years before the start of the research and 2) the high population density of sand flies, according to information from the Center of Zoonosis Control of the Municipal Secretary of Health, which was based on an entomologic survey carried out between January 2008 and July 2009. Field activities (population dispersion and longevity) involved the capture, marking with fluorescent powder, release, and recapture of specimens.

Population Dispersion. The dispersion experiments were conducted between November 2009 and 2010 November, with a 1-mo interval between each experiment, totaling three experiments in the rainy season and three in the dry season. The insects were captured using a hand-held electric aspirator between 1800 and 2300 hours in the area surrounding a residence with a chicken coop (site 1, Fig. 1B). The specimens were collected and transferred to a polystyrene foam container lined on the bottom with a fine layer of wet plaster and with lateral openings covered with a metal screen, similar to that described by Casanova, Costa, and Natal (2005). The sand flies were marked with fluorescent powder (BioQuip, Gardena, CA) and released the same night. Different colors were used for each experiment.

Attempts at recapture were performed once a week for four consecutive weeks in the areas surrounding 13 residences, including the release site. These residences were sampled radially with buffers of 50, 100, and 200 m on a cartographic base of the region, starting from the residence at which the insects were released. At each site, three automatic light traps (modified Centers for Disease Control and Prevention light-trap) spaced 5 m apart were deployed between 1800 and 0700 hours, totaling 39 traps. For the identification of the marked specimens, all sand flies collected were viewed in a camera obscura under ultraviolet light for the determination of fluorescence.

As the region was an urban area with the division of lots and well-defined public streets, it was not possible to sample the sites exactly within the buffer zones of 50, 100, and 200 m, as some sites were initially located on public streets. Moreover, the denial of some residents was another factor that altered the initial distances. In such cases, the next closest home was sampled.

An IKONOS-2 image from 5 March 2006 of the urban area of Campo Grande, Mato Grosso do Sul, with a spatial resolution of four meters for multispectral bands and 1 m for the panchromatic band, was used as the cartographic base (Fig. 1B). The use of a global positioning system was not necessary, as the image was georeferenced. The measurement of the distances between sites during the recapture attempts was determined on the panchromatic band using the PCI Geomatica program, version 9.1.

Climatic data (temperature, relative humidity, rainfall, and wind speed) for the months of population dispersion study were obtained from the meteorological database of the Center for Monitoring Weather, Climate, and Water of Mato Grosso do Sul (Cemtec). With the exception of rainfall, which was considered as the total value for each month, we calculated the monthly arithmetic average of the other variables.

Daily Survival and Population Size. Sand fly longevity and population size were estimated in an experiment conducted in January 2012. The aforementioned capture-mark-recapture method was used, but the recapture attempts were carried out over a 15-d period using 10 automatic light traps deployed at a single residence.

Data Analysis. The recapture rates and dispersion distances were estimated based on the methods described by Killick–Kendrick et al. (1984), Alexander and Young (1992), and Morrison et al. (1993). The number of marked individuals recaptured in each residence was transformed to ln (y + 1) and regressed as a function of the distance of the trap from the release site (Casanova et al. 2005). The long recapture period allowed observations on longevity. Thus, the total number of recaptured specimens was transformed in ln (y + 1) and regressed as a function of time in days. The linear correlation analysis (Spearman correlation coefficient) was used to evaluate the association between the numbers of recaptured insects (males and females) with climatic variables.

Regression analysis was undertaken to estimate daily survival. For such, the daily survival of males and females was considered constant throughout the postrelease time and was calculated based on the number of recaptured insects regressed and transformed by ln (y + 1) as a function of postrelease days (Nelson et al. 1978, Casanova et al. 2009, Galati et al. 2009):

$$\ln mt = \ln (M_0 r) - t \ln S$$

in which mt is the number of marked insects recaptured on each day, M_0 is the number of marked and released insects, r is the recapture rate, S is the daily survival rate, and t is time since release.

The survival rate was calculated by the expression $S = eb$, in which e is the base of the natural logarithm and b is the regression coefficient (Nelson et al. 1978). Population size was calculated using the Lincoln index adjusted for low recapture rates, with the inclusion of the survival rate. Monthly population size and variance were calculated by the mean of daily estimates, using the following formula:

$$N_t = (n_t + 1)\, M_t / (m_t + 1), \text{ with } M_t = (M_0 - \Sigma\, m_t)\, S^t$$

and variance was determined as follows:

$$\mathrm{Var}\, N_t = (M_t)^2\, (n_t + 1)\, (n_t - m_t) / (m_t + 1)^2\, (m_t + 2)$$

in which N_t is the absolute population estimated, n_t is the number of specimens captured, m_t is the number of marked and recaptured specimens, M_t is the number of marked specimens that remained in the population, M_0 is the number of marked and released specimens, S is the daily survival rate, and t is time on days (Casanova et al. 2009, Galati et al. 2009). Statistical analysis described was performed using the SPSS version 10.0 (Cary, NC).

Table 1. Number and recapture rates of *Lu. longipalpis* according to sex and distance (by buffer) during dispersal experiments, 2009–2010

Experiment buffers	*N* released	*N* (%) recaptured		Total
		Male	Female	
A	537			
0		8[c] (1.49)	—	8 (1.49)
50		2[a,c] (0.37)	—	2 (0.37)
100		—	—	—
200		—	—	—
Total		10 (1.86)	—	10 (1.86)
B	415			
0		28[a] (6.75)	22[a] (5.30)	50 (12.05)
50		2[b] (0.48)	1[b] (0.24)	3 (0.72)
100		—	—	—
200		—	—	—
Total		30 (7.23)	23 (5.54)	53 (12.77)
C	330			
0		1[d] (0.30)	—	—
50		—	—	—
100		—	—	—
200		—	—	—
Total		1 (0.30)	—	1 (0.30)
D	250			
0		20[d] (8.00)	11[a] (4.40)	31 (12.40)
50		—	—	—
100		—	—	—
200		1[a] (0.40)	1[a] (0.40)	2 (0.80)
Total		21 (8.40)	12 (4.80)	33 (13.20)
E	367			
0		5[a] (1.36)	—	5 (1.36)
50		1[a] (0.27)	—	1 (0.27)
100		—	—	—
200		—	—	—
Total		6 (1.63)	—	6 (1.63)
F	604			
0		3[d] (0.49)	—	—
50		—	—	—
100		—	—	—
200		—	—	—
Total		3 (0.49)	—	4 (0.49)
Total		71 (2.83)	35 (1.40)	106 (4.23)

[a] Recaptured in first week.

[b] Recaptured by second week.

[c] Recaptured by third week.

[d] Recaptured by fourth week.

Results

In total, 2,503 sand flies were captured, marked, and released during the six dispersion experiments. One hundred six were subsequently recaptured, corresponding to a recapture rate of 4.23%. Among the recaptured specimens, 67% were males and 33% were females. In total, 92.45% were recaptured at the release site, 6.66% were recaptured within a 50-m radius, and 1.88% were recaptured within a 200-m radius. Marked specimens were captured at 65.9, 55, 49.2, 241, and 165 m. Table 1 shows the number and percentage of recaptured sand flies according to sex and recapture distance, along with observations on the longevity of

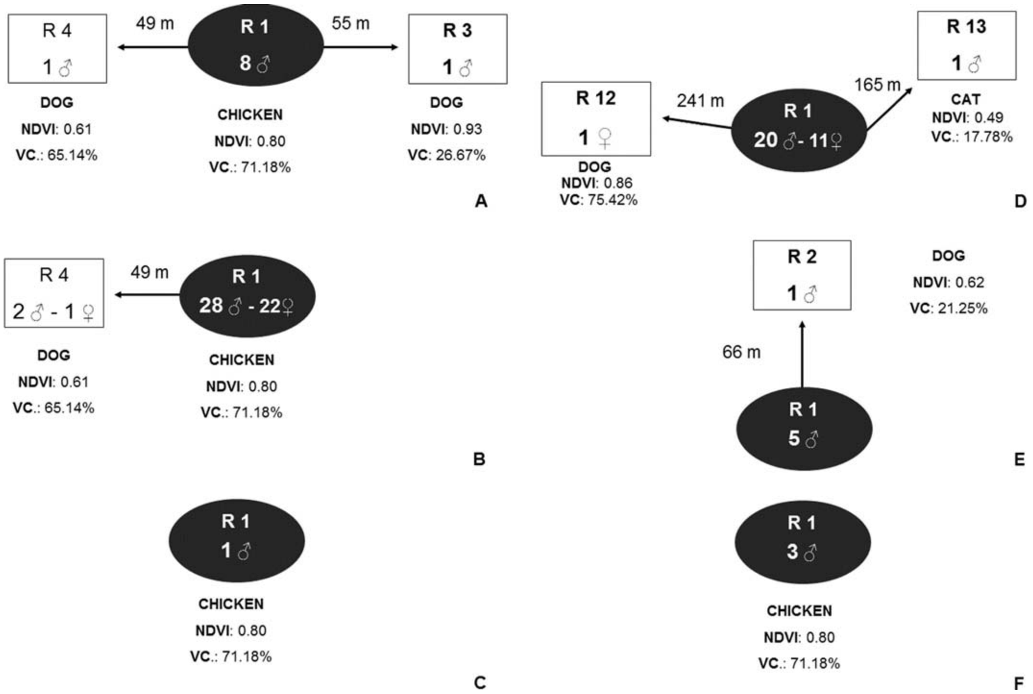

Fig. 2. Dispersion experiments, November 2009 to November 2010. R = residence; NDVI = normalized difference vegetation index; VC = vegetation cover (Oliveira et al. 2012).

Lu. longipalpis. The presence of domestic animals (chickens, dogs, and/or cats) was observed at all residences, with the exception of residence 11.

In the first experiment (A), which was conducted in November and December 2009, 537 sand flies were captured, marked, and released, with recapture occurring at sites 1, 2, and 3 (Fig. 2A). In the second experiment (B), which was conducted in January and February 2010, 415 sand flies were captured, marked, and released, with recapture occurring at only two residences (1 and 4) (Fig. 2B). In the third experiment (C), which was conducted in March and April 2010, no population dispersion was determined and only one of the 330 specimens released was recaptured at site 1 (Fig. 2C). Experiment D, which was conducted in May and June 2010, had the largest recapture rate among the six experiments. In total, 250 sand flies were captured, marked, and released, with recapture occurring at three sites (1, 12, and 13) (Fig. 2D). Moreover, the largest dispersion distances also occurred in this experiment, with one male and one female recaptured 14 d after release at 165 and 241 m (sites 13 and 12), respectively. In the fifth experiment (E), which was conducted in August and September 2010, 367 sand flies were captured, marked, and released, with recapture occurring only at sites 1 and 2 (Fig. 2E). In the sixth experiment (F), which was conducted in October and November 2010, 604 sand flies were captured, marked, and released. Population dispersion was also not determined in this experiment (Fig. 2 F). Figure 3 displays all dispersion directions.

The number of recaptured individuals at each residence [transformed in ln $(y + 1)$] did not decrease significantly [$\ln(y + 1) = -0.0105x + 2.4986$; $P = 0.209$] as a curvilinear function of trap distance from release site (Fig. 4A).

Regarding the time elapsed until recapture during the dispersion experiments, 50.94% of the specimens were recaptured within the first week. In the following 3 wk, 20.75, 15.09, and 13.21% were recaptured, respectively. The number of recaptured specimens transformed into ln $(y + 1)$ did not decrease significantly [$\ln(y + 1) = -0.06x + 4.2211$; $P = 0.074$] as a curvilinear function on time in days (Fig. 4B).

During November 2009 to November 2010, the mean maximum, mean, and mean minimum temperatures were 30.1, 23.7, and 19.0°C, respectively, with mean relative humidity of 66.2%, rainfall of 1,637.2 mm and mean wind speed of 33.67 m/s with predominate direction to north–east (NE) and south–west (NW). There was no significant association between of recaptured sand flies and the climatic variables.

For the estimate of daily survival and population size, 851 sand flies (793 males and 58 females) were marked and released. The recapture rate for males was 2.39%. No females were recaptured in this experiment. One male was recaptured 14 d after release. The number of recaptured specimens transformed into ln $(y + 1)$ decreased significantly as a curvilinear function of time in days after release. The daily survival rate calculated based on regressions of the number of marked insects recaptured on the 15 successive days after

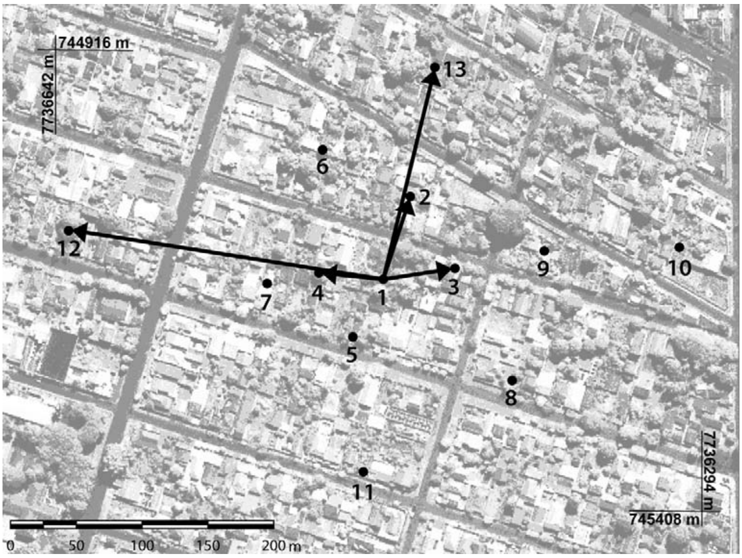

Fig. 3. Dispersion directions of *Lu. longipalpis*, November 2009 to November 2010.

release was 0.897 for males. The absolute size of the male population of *Lu. longipalpis* (estimated using the Lincoln Index method) in January 2012 was 10,947.127 (SD = 7,528.646).

Discussion

The present investigation, carried out in a completely urban area endemic for VL, is a pioneering study, as the majority of previous experiments involving capture, mark, and release procedures have been carried out in wild areas with and without anthropogenic influence. Thus, it is important to consider biological differences between species as well as variations in the vegetation, climate, and host species in the different regions studied (Alexander 1987).

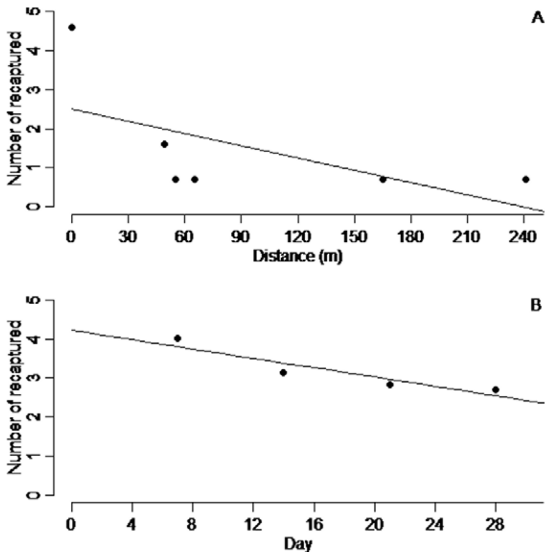

Fig. 4. Relationship between total number of sand flies recaptured at different distances from release site (A) and as function of time in days (B), November 2009 to November 2010.

The initial maximal distance of 200 m established in the current study was based on previous investigations carried out in the Americas that describe movements within a smaller radius than this figure (Alexander and Young 1992, Casanova et al. 2005, Chaniotis et al. 1974). Based on two previous studies carried out in Campo Grande with *Lu. longipalpis,* which report high recapture rates of 99.4% (Oliveira 2006) and 75% (unpublished data) at the release site within the first week, the decision was made to await a period of 7 d after the release of the insects before beginning the recapture procedures. If recapture procedures had begun on the day after release, the insects may not have had enough time to disperse in their natural pattern.

The recapture rate during the dispersion study was 4.23% (106/2503), ranging from 0.30 to 13.20% throughout the six experiments. These data corroborate findings described in the literature for species in both the Old World and the Americas, with recapture rates ranging from 0.1 to 13.0% (Alexander 1987; Alexander and Young 1992; Chaniotis et al. 1974; Casanova et al. 2005, 2009; Galati et al. 2009; Killick–Kendrick et al. 1984; Quate 1964). Considering only data on the dispersion of *Lu. longipalpis,* the findings of the current study are also in agreement with those described by Morrison et al. (1993) in a study carried out in Colombia, who report an overall recapture rate of 5.5%, ranging from 2.2 to 13.0%.

The predominance in the percentage of males over females in all phases of the study corroborates data described by Morrison et al. (1993) for *Lu. longipalpis* as well as data described for *Ny. neivai* (Casanova et al. 2005, 2009; Freitas et al. 2009; Galati et al. 2009).

However, this finding differs from data described by Yuval et al. (1988), who studied the dispersion of *Phlebotomus papatasi* Scopoli in western Asia. A number of studies suggest that the use of light traps may lead to the capture of more male specimens, but, depending on the species studied, a predominance of females over males has been observed on some occasions using this same trapping method (Barreto 1943, Aguiar et al. 1985, Yuval et al. 1988).

In the current study, the site of capture, marking, and release also accounted for 92.45% off all recaptured specimens. This tendency on the part of sand flies to remain in the release area is also reported by other authors, such as Chaniotis et al. (1974), Alexander (1987), and Oliveira (2006), who respectively report that 80.6, 50.8, and 99.4% of the specimens were recaptured at the release site. These data suggest that sand flies exhibit little dispersion activity and remain at the same site because of the presence of shelter and food, as the presence of domestic animals associated with precarious local hygiene conditions contributes toward the maintenance of a high population density of *Lu. longipalpis* (Ximenes et al. 1999). The high rates of positivity for the blood of birds in the digestive tract of females recaptured at the release site in a dispersion study carried out in 2005 (Oliveira et al. 2008) provides additional support to this hypothesis, as there was an abundance of food sources at the site.

The high rate of males among the recaptured specimens and among the nonmarked specimens captured at residence 1 suggests that this site has ecotopes for lekking (Alexander and Young 1992), as the main focal points of this type of behavior are shelters for domestic animals, especially chicken coops (Quinnell and Dye 1994). Thus, lekking is one of the hypotheses that may explain why the sand flies remained in the sites at which they were marked and release, as the area surrounding the residence has both a chicken coop and a large amount of vegetation, which protects the soil from exposure to direct sunlight, thereby maintaining local moisture and permitting this environment to serve as a shelter and possibly a nursery for this dipteran (Oliveira et al. 2012). There is also the possibility of familiarization with the environment, spatial memory and fidelity to the host, which could orient sand flies with regard to recognizing and remaining in locations in which there is an availability of sources of blood (Kelly and Dye 1997, Campbell–Lendrum et al. 1999, Freitas et al. 2009).

The maximal dispersion distances were 165 and 243 m, reached by one male and one female, respectively, 14 d after release. Chaniotis et al. (1974) report that 87.5% of sand flies were recaptured within a 57-m radius, with a maximal distance of 200 m reached by a female specimen of *Lutzomyia shannoni* Dyar 24 h after release. Also working in forest areas, Alexander (1987) confirmed that the dispersion distance did not surpass 200 m. Galati et al. (2009) describe similar findings for *Nyssomyia intermedia* Lutz & Neiva. Studies by Morrison et al. (1993) involving populations of *Lu. longipalpis* in Colombia demonstrated that 48% of the marked specimens were recaptured between 100 and 300 m and 3% were recaptured at a distance of 500 m or more, with one female reaching 960 m 48 h after release. In Brazil, the longest distance reported was 700 m for *Lu. longipalpis* (Dye et al. 1991) and 520 m for *Ny. neivai* (Galati et al. 2009). In the Old World, studies describe distances of up to 2,200 m for *Phlebotomus ariasi* Tonnoir (Killick–Kendrick et al. 1984), 730 m for *Phlebotomus orientalis* Parrot (Quate 1964), and 289 m for *Phlebotomus longipes* Parrot & Martin (Foster 1972).

Although some studies showed that the decrease in the abundance of sand flies is associated to the high wind speed (Oliveira et al. 2013, Ximenes et al. 2006, Zeledón et al. 1984), there is as yet no proof that the dispersion of these vectors occurs passively through the force of the wind (Killick–Kendrick et al. 1984). Possibly this relationship is also true for the dispersal, because these insects could remain housed in the occurrence of high wind speeds. However, one must consider the hypothesis that breezes can carry volatile amines emitted from vertebrate hosts, which could influence the dispersal of vectors.

As in the previously cited studies, the largest percentage of recaptures occurred in the same area as the release site, demonstrating that dispersion exhibited a discreet, focal pattern. However, some specimens were recaptured in the 50 and 200 m buffer zones, despite the physical barriers that are characteristic of the urban environment, such as buildings, walls, and vegetation-free areas exposed to direct wind and sunlight. This has epidemiological importance, as the capacity to reach large distances could hamper control measures.

Studies carried out in Ethiopia by Foster (1972) revealed that nonfed females dispersed more, followed by males and engorged or gravid females. In agreement with this finding, the greatest dispersion distance achieved in the current study was by a nonfed female. According to Killlick–Kendrick et al. (1984), one of the hypotheses for explaining the long distances traveled by females is the search for a food source. In the current study, all sites in which sand flies were recaptured had domestic animals (chickens, dogs, and/or cats) and large amounts of vegetation in the surrounding area (Oliveira et al. 2012a).

The longevity of adult sand flies under natural conditions in wild or urban environments is virtually unknown, but there are indications that both sexes can survive as many as 20–30 d (Brazil and Brazil 2003). For neotropical sand flies of the species *Ny. neivai,* survival of 14 d in nature is described (Casanova et al. 2005). Chaniotis et al. (1974) recaptured specimens of *Lu. shannoni* and *Lu. trinidadensis* Newstead up to 15 d after release. These findings are similar to those reported in the current study for *Lu. longipalpis,* in which a total of 71.69% of recaptures occurred within 14 d after the release of the marked specimens.

It should be stressed that the field experiment did not allow the determination of the age of the marked sand flies. However, it is likely that the natural mortality of these insects occurred throughout the recapture process, which affected the number of insects recaptured (Freitas et al. 2009). Nonetheless, the recapture rates were 15.09 and 13.21% on days 21 and 28 during the dispersion study, respectively. Only Oliveira (2006) reports a similar recapture time as that used in the current study. Thus, this information represents the longest survival period for *Lu. longipalpis* in the urban environment described in nature. This is an aggravating factor when considering the time needed for the evolution of the parasite in the vector and the occurrence of more than one gonotrophic cycle in this species (Ferro et al. 1995), allowing the occurrence of multiple blood meals and, consequently, a longer period of transmissibility of the parasite.

As 91% of the recaptures in the six dispersion experiments occurred at the release site, the decision was made to conduct the last experiment for the estimate of daily survival and population size at this site alone. In a previous study, daily estimated survival for *Ny. neivai* was 0.681 for males and 0.667 for females and the absolute population ranged from 861 to 4,612 males and from 2,187 to 19,739 females from May 1999 to April 2000 (Casanova et al. 2009). Similar data are described for *Ny. intermedia* and *Ny. neivai* by Galati et al. (2009). Although it was not possible to estimate the daily survival rate and population size for females specimens of *Lu. longipalpis* because of the nonrecapture of this sex and the small amount of females released, one female was recaptured 14 d after release during the dispersion experiments. As previous studies carried out in the same city also report a higher proportion of male specimens (Oliveira et al. 2006; Oliveira et al. 2012, 2013), one may infer that the local population is truly mainly composed of males.

Drastic environmental changes because of human actions, such as the rapid process of urbanization seen in emerging countries like Brazil, have changed the ecology of some species of sand flies, with a consequent change in the eco-epidemiology of VL, which has had a significant impact on distribution of the disease and mortality rates since the 1980s (Werneck 2008). The urbanization process in Brazil gained intensity beginning in the 1950s because of the industrialization and modernization of agrarian activities. However, this process was not uniform throughout the country and occurred without due planning, with the unregulated occupation of forest areas and destruction of natural habitats for the breeding of the vector and wild reservoirs, which has favored direct contact between humans, vectors, and reservoirs. This situation is associated with the dietary eclecticism of *Lu. longipalpis* and its ease of adaptation to domestic conditions, which may have contributed to the urbanization of VL (Rangel and Vilela 2008).

The control of vectors is one of the main aspects of the management of infectious vector diseases. Moreover, dispersion and longevity are among the factors that indirectly determine the dissemination of the disease. Thus, the dispersion behavior encountered in the current study underscores the importance of vector control measures based on the periodic application of insecticides with residual effects in locations with records of autochthonous cases of the disease to reduce contact between the vector and the human population.

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