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The Distribution and Abundance of Triatomine Insects, Potential Vectors of Chagas Disease, in a Metropolitan Area in Southern Arizona, United States

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ABSTRACT Triatomine insects are a problem for human health in southwestern United States because of the moderate-to-severe allergic reactions their bites can cause and because they are potential vectors of Chagas Disease. Although both infected insects and wild mammalian reservoirs are plentiful in southern U.S., only seven cases of autochthonous transmission (plus 16 new presumed cases) of this disease have been reported to date. Therefore, the purpose of this study was to investigate triatomine distribution and abundance in a metropolitan area in southern Arizona. Species, life-stage, locality, and date of collection were recorded for 1,878 triatomine insects collected during 4 yr inside and around houses. For both sexes of the most abundant species, *Triatoma rubida* (Uhler) (>95% of triatomines collected), dispersal followed a typical year-to-year pattern: dispersal started at the beginning of May and peaked during the first-second week of June. *T. rubida* was found widely distributed in suburban areas. Triatomines of the two less abundant species, *T. recurva* (Stal) and *T. protracta* (Uhler), were collected in all suburban areas throughout the 4-yr survey. All of these population characteristics were observed both at a large (i.e., all collection sites pooled) and a small (i.e., single collection sites) scale. In total, ≈55–60% of the triatomines were collected inside houses, and 30–35% of those were found in or near beds; thus, it is likely that they fed on humans. To our knowledge, this study is the first comprehensive multi-year analysis of triatomine distribution and abundance in the U.S., providing data that allow inferences about risks to human health.

KEY WORDS triatomine, dispersal, U.S.A., Chagas disease, allergy

Blood-sucking bugs of the family Reduviidae (Triatominae), commonly known in the United States as kissing bugs, are problematic for human health in the southwestern U.S. because of the moderate-to-severe allergic reactions their bites can cause, including anaphylaxis (Lynch and Pinna 1978, Pinna et al. 1986, Klotz et al. 2010). Triatomines are best known, however, as vectors of Chagas Disease, a potentially deadly disease caused by the protozoan parasite *Trypanosoma cruzi*, which is endemic in Mexico and Central and South America (World Health Organization 2011). In the U.S. both infected triatomines (Wood 1942, 1943b; Wood and Wood 1961; Kjos et al. 2008a; Reisenman et al. 2010; Bern et al. 2011) and wild mammalian reservoirs (e.g., packrats, mice, armadillos, raccoons, squirrels, bats, opossums, skunks, foxes, and dogs) are plentiful (Packchianian 1942; Wood 1942, 1943b, 1949; Wood and Wood 1961; Ryckman 1986; Pung et al. 1995; Yabsley and Pittman 2002; Shadomy et al. 2004; Rosypal and Tidwell 2007; Brown et al. 2010). Nevertheless, only seven autochthonous cases of Chagas

Disease have been reported to date in the U.S., all in the southern half of the country (Woody and Woody 1955, Schiffler et al. 1984, Ochs et al. 1996, Herwaldt et al. 2000, Dorn et al. 2007, Bern et al. 2011). A recent study based on data from U.S. blood banks added 16 additional cases of presumed autochthonous transmission (Cantey et al. 2012).

In the U.S., and particularly in Arizona, kissing bugs are becoming an important health problem because human populations are rapidly expanding into triatomine habitats. From late May through the mid-July, hungry adult triatomines leave the nests of their hosts. In southern Arizona triatomines live in close association mainly with the white-throated woodrat, *Neotoma albigula* (Wood 1949, Ryckman 1986), and disperse mostly by flying to colonize new areas. Starvation may be the primary stimulus that initiates flight (Wood 1950, Ekkens 1981, Lehane et al. 1992), and most flights occur during the first 4 h after sunset (Ekkens 1981). The insects are attracted to houses by porch and patio lights, or lights shining through windows (Wood 1941, 1950; Ekkens 1981). Once inside houses they find humans and pets using host-derived odor cues (Barrozo and Lazzari 2004, Guerenstein and Lazzari 2010).

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Table 1 Numerical description, on a yearly basis, of the sample used for this study

Year	No. of insects	No. of collection sites/geographical area						No. of insects/collection site		
		C	N	S	E	W	Total	Mean $\pm$ SE	Range	Median
2006	138	1	7	4	3	1	16	8.8 $\pm$ 5.1	1–84	2.5
2007	555	6	68	11	18	4	107	5.1 $\pm$ 1.3	1–130	1
2008	649	2	36	13	14	8	73	8.0 $\pm$ 2.4	1–134	2
2009	536	6	68	13	18	13	118	4.5 $\pm$ 0.9	1–93	2

Geographical areas are: central Tucson (C), North (N), South (S), East (E), and West (W).

Although triatomines can be found inside houses mostly from May through July in southern Arizona (Wood 1950, 1957; Reisenman et al. 2010), they appear to have a low capacity for establishing colonies inside houses (Zeledón and Rabinovich 1981).

We recently reported that 41.5% of a large sample of *Triatoma rubida* (Uhler) (the most abundant triatomine species in southern Arizona) collected in metropolitan Tucson, AZ, were infected with *T. cruzi* (Reisenman et al. 2010). Notwithstanding, this finding and reports that *T. rubida* readily feeds on humans (Stevens et al. 2012), no cases of Chagas Disease have been reported to date in Arizona. This might be because of the relatively low vectorial capacity of *T. rubida* in comparison with that of other triatomine species (Reisenman et al. 2011). Although some of the strains of *T. cruzi* present in U.S. can be highly pathogenic to dogs and other mammals (Barr 2009, Cura et al. 2010), it is not known whether those strains are also pathogenic to humans.

Given the importance of triatomines for human health in southern Arizona, both as cause of allergic reactions and as potential vectors of Chagas Disease, the aim of this investigation was to compile a comprehensive account of the species distribution and abundance of triatomines over a 4-yr period. To our knowledge, this is the first large-scale study of this kind in the U.S.

Materials and Methods

Triatomine insects were obtained by issuing public requests asking residents of metropolitan Tucson (32° 14'25" N, 110° 56'43" W), AZ, to collect kissing bugs they might find inside and/or around their houses. Only insects collected within a 24–32 km radius from those coordinates, plus an extended 48 km area south-east thereof, were included in this study. Insects that reach houses, as opposed to those directly collected from nests of wild animals removed from human households, are of greatest epidemiological importance because they have the highest likelihood of contact with humans.

More than 99% of the insects were collected in suburban Tucson. The landscape in this area (that is part of the lower Sonoran desert) is dominated by legume trees (e.g., mesquite, Palo Verde), large columnar cacti (Saguaro), creosote, triangle-leaf bur-sage, etc. The climate is semiarid with bimodal precipitation (half of the annual precipitation occurs in July through August, and the other half from mid-

November to mid-April). June is the driest and hottest month, with daily temperatures averaging 39°C. Houses in suburban Tucson maybe aggregated in communities or isolated from one another, but in most cases they are surrounded by wild-landscape and native fauna, and usually in close proximity to the nests of packrats. House owners may have dogs that in some cases spend time outdoors, possible in contact with wildlife. The north part of the area of the study is the most densely populated.

Collectors were provided with an informative flyer with pictures of the three species of triatomines found in the area. They were always instructed to use a container and to avoid handling the insects with bare hands, and were informed about Chagas Disease transmission. For each kissing bug provided to us, we recorded, whenever possible, the collection site (address), species, stage (if adults, sex), and date of collection as well as any other additional information provided by the collector (e.g., in which part of the house the insect was collected, if the collector was bitten, etc.). Collectors varied throughout the period of study. All material that had been in contact with field-caught triatomines was disinfected with absolute ethanol or autoclaved if possible. Temperature data were downloaded from the Website of the National Weather Service Forecast Office (Tucson, AZ; <http://www.wrhn.noaa.gov/twc/climate/reports.php>). Daily minimum temperatures were averaged over 7 d from 17 March to 30 August, and from 8 May to 13 August of each year (Fig. 3; Supp. Fig. 1B [online only]). Data from a total of 1,878 kissing bugs collected in 2006–2009 was included in this study (Table 1). Geographical areas were determined using a compass map with cardinal directions North (N), South (S), East (E), and West (W); the inter-cardinal directions were NE, NW, SE, and SW. Because complete information about each collected insect was not always obtained (for instance, the locality or the date of collection), the number of insects included in the different analyses presented throughout this manuscript might be different. Differences between groups (e.g., sexes, species) or expected proportions (i.e., male to female ratio) were analyzed using χ^2 tests and were considered statistically significant if $P < 0.05$.

Results

Sample Description. Table 1 shows the total number of insects collected per year, the number of collection sites in each geographical area, and the num-

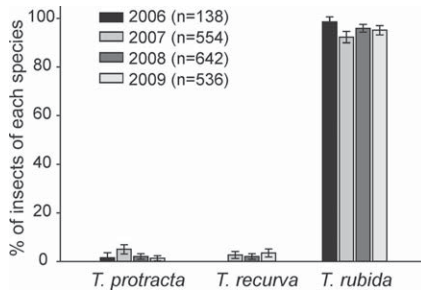


Fig. 1. Percentage of insects of each species collected in each year. Vertical lines indicate 95% CI. Numbers in parentheses indicate the number of insects collected.

ber of insects collected per collection site. The sharp increase in the number of collection sites (from 16 in 2006 to 107 in 2007) resulted from an intensification of recruiting efforts. Each collector (also referred to as “collection site” throughout this report) provided a variable number of insects, with many collectors providing as few as one insect and single collectors providing ≈ 130 insects in 2007 and 2008. Most collectors, however, provided 1–2 insects (Table 1, last column). In the rare case in which the same collector collected insects in two different localities, those were referred to as two different collection sites. It is likely that collection effort or consistency varied among collectors. The majority of collection sites were north of the city, probably owing to a higher human population density in this area; some of the collections sites were represented in all years.

Species Abundance and Sex Distribution. Three triatomine species can be usually found in Tucson, AZ: *T. rubida*, *T. recurva* (Stal), and *T. protracta* (Uhler). Figure 1 shows the percentage of adult kissing bugs of these three species collected during 2006–2009. Coincident with previous reports (Bice 1964, Ekkens 1981), the most common species was *T. rubida* ($95.1 \pm 1.8\%$ of insects collected; average $\pm$ SE; $n = 4$ yr).

For the rest of our analyses we focused on adults, the most common stage found in households (96.2% of the insects collected were adults). Although adult insects most likely colonize houses by flying, they can also do so by walking. Among adults, those that might pose a high colonization risk are females, because they can contribute to the establishment of triatomine populations in houses given their capacity to lay eggs (indeed some dispersing females carried fertile eggs). Figure 2 shows the female-to-male ratio for the three species (the sex ratios for *T. recurva* and *T. protracta* could not be statistically analyzed for the 2006 data because only a few specimens were collected). For the most abundant species, *T. rubida*, the sex ratio of females to males significantly deviated from the 1:1 expected ratio only in 2006 (more females than males were collected; $P < 0.05$, χ^2 test; Fig. 2A). For *T. protracta*, significantly more males than females were collected in 2007 ($P < 0.05$; Fig. 2B), and a larger proportion of males were also collected in 2009 ($P > 0.05$ probably because of the low total number of

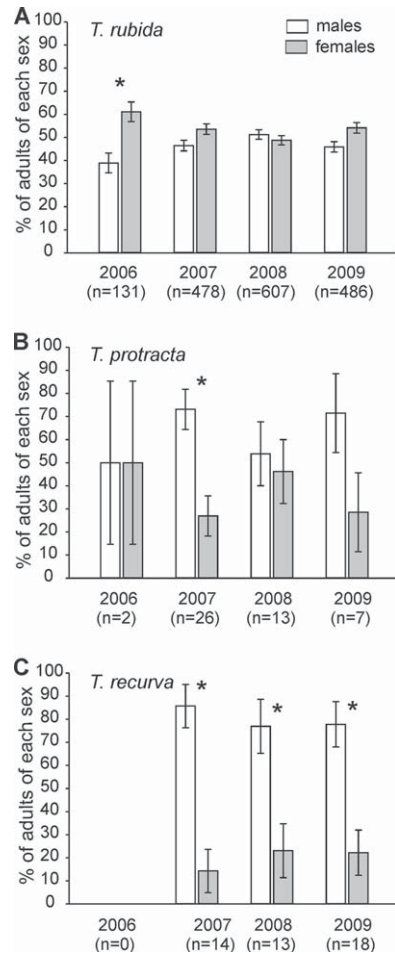


Fig. 2. Percentage of females and males of each species (A: *T. rubida*, B: *T. protracta*, C: *T. recurva*) collected each year. Vertical lines indicate 95% CI. Numbers in parentheses indicate the numbers of adult insects collected. Asterisks indicate significant differences between the number of females and males collected in a given year (χ^2 tests; $P < 0.05$).

specimens collected). In the case of *T. recurva*, significantly more males than females were collected in 2007–2009 ($P < 0.05$; Fig. 2C).

Temporal Dynamics of Insect Dispersal. Figure 3 shows the number of adult insects collected per week in 2006–2009 during a typical dispersal season (defined from 5/8 to 8/13). In 2006–2008 most insects dispersed during the first 2 wk of June (weeks 4–5; Fig. 3A–C), which was likely because of temperature increases above a critical minimum (traces in Fig. 3A–C) (Gurevitz et al. 2006). In 2009, the minimum temperature remained lower (under $\approx 20^\circ\text{C}$) for a longer time period, and the monsoon rains did not follow their typical pattern, which likely influenced triatomine dispersal (Fig. 3D). On average, however, a higher proportion of the insects dispersed during weeks 4–5 in all 4 yr (Supp. Fig. 1A [online only]). For the most abundant species, *T. rubida*, there were no differences

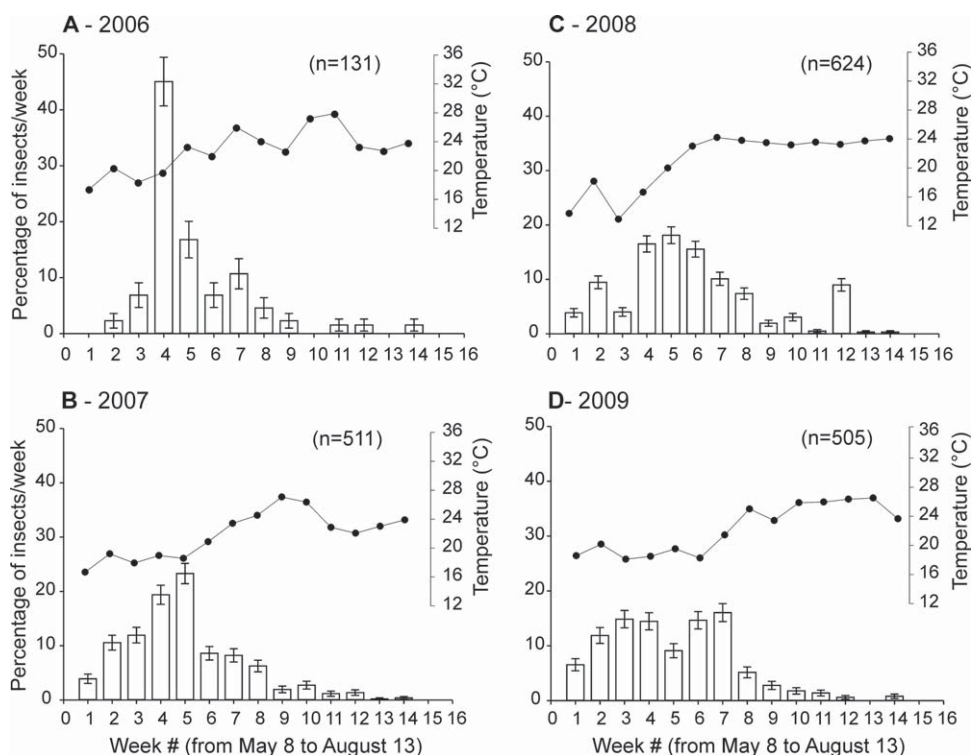


Fig. 3. Temporal dynamics of triatomine dispersal (all species and stages). Each panel shows the percentage of insects (left axis, bars) collected per week during the 2006 (A), 2007 (B), 2008 (C), and 2009 (D) dispersal seasons (defined here as 8 May through 13 August). Vertical lines indicate 95% CI. The traces show the minimum daily temperature averaged over 7 d during the same time periods (right axis). The number insects collected during each year's dispersal season is shown in parentheses.

in the temporal pattern of male and female dispersal (data not shown).

In all years (2007–2009) the first triatomines collected were from one of the less abundant species, *T. protracta* (Fig. 4; only flying adults were considered in this analysis). The first specimens of this species were captured as early as 17 March (in 2007). In any given year, the first specimen of the other less abundant

species, *T. recurva*, was captured as early as 23 April and, in the case of the most abundant species, *T. rubida*, in 5 May. On average, by mid-late May, half of all specimens of *T. protracta* and *T. recurva* already had been collected, respectively (Fig. 4). *T. rubida* dispersed later, with half of all specimens (on average) collected by mid-June (Fig. 4). These results suggest that perhaps both *T. protracta* and *T. recurva* can fly at lower temperatures than *T. rubida*.

To analyze further the temporal dynamics of dispersal, we selected a subset of collection sites ($n = 6$ sites) where >25 insects (69.7 ± 18 ; average $\pm$ SE) were collected during at least six different weeks in a single dispersal season (2008). These six collection sites were distributed across three different geographical areas (two in SE, two in W, two in NW). Again, a peak of dispersal was observed at the end of May/beginning of June (weeks 4–5 in Supp. Fig 1B [online only]). We also analyzed the year-to-year variation in the temporal pattern of dispersal at a single collection site (in the SE area) where a large number of insects were collected. Again, in all 3 yr (2007–2009) most insects were collected in May and June (Supp. Fig. 1C [online only]).

Species Distribution. Figure 5 shows the geographical distribution of the three triatomine species collected in 2007–2009 (data for 2006 was not included in

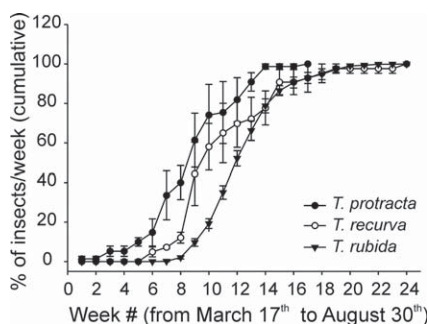


Fig. 4. Cumulative percentage of adult insects of each species collected from 17 March (when the first dispersing adult appeared in any given year) through 30 August (average $\pm$ SE; $n = 3$ yr; 2007–2009). An average ($\pm$ SE; $n = 3$ yr) of 15 ± 5 *T. protracta*, 14 ± 1 *T. recurva*, and 528 ± 39 *T. rubida* were collected during that time period.

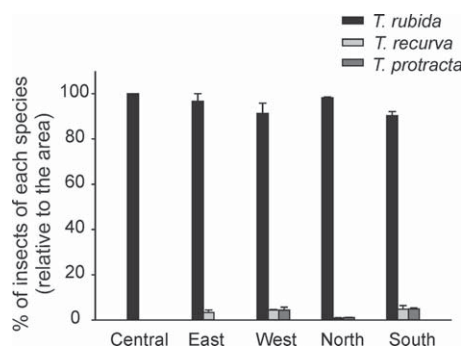


Fig. 5. Percentage of insects (average $\pm$ SE; $n = 3$ yr) of each species collected in each area in 2007–2009.

this analysis because a very small number of insects of species other than *T. rubida* were collected). *T. rubida* was found widely distributed (black bars), and surprisingly, a few insects of this species were captured in central Tucson in all years. The numbers of insects collected in each area per year ($n = 3$ yr) were (average $\pm$ SE): 7 ± 3 in Central Tucson, 22 ± 6 in E, 109 ± 14 in W, 273 ± 10 in N, and 168 ± 31 in S. These differences in the average number of insects collected do not necessarily indicate a higher abundance (except in Central Tucson, where triatomines are rarely found) but possibly reflect a higher number of insects collected per collection site (or a higher number of collection sites) in a given area (e.g., N). We also analyzed the year-to-year variation in species abundance in two sites (one in SE and one in W) where a large number of insects (70 ± 15 insects/year) were collected over three consecutive years (not shown). At both sites and in all years, *T. rubida* was the most abundant species, and the relative species abundance followed a similar year-to-year pattern.

Insect Distribution in Houses. Figure 6 shows where (within and/or around houses) insects were collected in 2008–2009. Because not all collectors provided this information, the sample used for this anal-

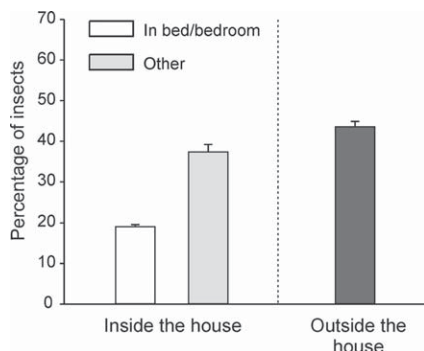


Fig. 6. Percentage of insects (mean $\pm$ SE; $n = 2$ yr) collected inside and outside houses in 2008–2009. White bars indicate the proportion of insects found in the bed/bedroom, light gray bars indicate insects found somewhere else inside the house, and dark gray bars indicate the proportion of insects found outside (but near) the house.

ysis was smaller than that presented in previous figures. In total, ≈ 55 –60% of the insects ($n = 419$ and 324 for 2008 and 2009, respectively) were found inside houses in both years, 30–35% of which were found in or near beds, and therefore it is possible that the insects fed on humans. Other common collection locations inside the house included living/family/dining rooms, kitchens, and less frequently, bathrooms. Furthermore, $\approx 25\%$ of the insects collected outside houses were found in patios or porches. Information about insect bites was not always obtained, but 20% ($n = 45$ collectors) and 29% ($n = 69$ collectors) reported having been bitten in 2008 and 2009, respectively.

Discussion

To our knowledge, this is the first comprehensive multi-year analysis of triatomine distribution and abundance in the U.S. In total, 1,878 triatomine insects (kissing bugs) were collected inside or near houses in a metropolitan area in southern Arizona over a 4-yr period, 96.2% of which were dispersing (likely flying) adults. We found that triatomine dispersal followed a characteristic year-to-year pattern that seemed to correlate (up to a certain point) with increases in nighttime temperatures (Fig. 3; Supp. Fig. 1B [online only]). The most abundant species, *T. rubida* ($>95\%$ of insects collected; Figs. 1 and 2), was found widely distributed in suburban Tucson and surprisingly, a few insects of this species were found in the city in all years (Table 1; Fig. 5). Dispersal of *T. rubida* started at the beginning of May and peaked during the first 2 wk of June (Fig. 3; Supp. Fig. 1 [online only]), and continued through late July or early August. *T. protracta* and *T. recurva*, the two other less abundant triatomine species collected, began to disperse earlier (Fig. 4). Insects were rarely found inside houses at other times of the year. In total, ≈ 55 –60% of the insects were collected inside houses, and 30–35% of the insects were found in or near beds (Fig. 6). Twenty-five percent of collectors reported having been bitten.

The first reports on triatomines from southern Arizona date to the 1930s. Wehrle (1939) reported that winged adults invaded houses in the vicinity of packrat dens, apparently attracted by light. These dispersal flights were most numerous during May and June and persisted throughout the summer. At that time few people lived in triatomine habitats, but in the last two decades the population of metropolitan Tucson has grown rapidly with notable expansion into the surrounding area of Pima County and hence into triatomine habitats ($\approx 461,000$ as of 2010; Pima Association of Governments; <http://www.pagnet.org/Regional-Data/Population/tabid/104/Default.aspx>), considerably increasing human exposure and hence, human health risks.

Early reports showed that *T. rubida* was the most abundant species in the area (Kofoid and Whitaker 1936; Wehrle 1939; Wood 1943a, 1949) and that a variable percentage of insects (5–9%, detected using microscopic methods) were infected with *T. cruzi*

(Wood 1943b, 1949). A more systematic study of triatomine dispersal in southern Arizona using black-light traps was conducted in the early 1970s (Ekkens 1981). Although a large number of insects were captured in that study (1,058 insects captured over 134 nights in two summers), all specimens were collected in a single locality outside the city of Tucson. Again, in that study, the most abundant species was *T. rubida*, followed by *T. recurva* and *T. protracta*. An important consideration is that the species ratio can be affected by the collection method. Using light traps, one study found that the ratio of *T. rubida* to *T. protracta* was 51:1, while in the den of packrats (that are the likely hosts of these two species) the species ratio was 11:1 (Ekkens 1981). In our study, in which insects were most likely attracted to lights from houses, we found (over the course of 4 yr) a 37:1 *T. rubida* to *T. protracta* capture ratio, and a 41:1 *T. rubida* to *T. recurva* capture ratio (packrats do not appear to be the main hosts of *T. recurva*; Ekkens 1981). Another important consideration is that the species ratio also can vary with the specific locality within a region (Bice 1964). In our study, although *T. rubida* was the most abundant species ($\approx 95\%$ of insects collected), all three species were found throughout the area of study with the exception of central Tucson, where only *T. rubida* was collected (Table 1; Fig. 5).

Species abundance could be very important for human health should species differ in their allergenic and/or in their vectorial capabilities. The bites of both *T. rubida* and *T. protracta* can cause anaphylaxis, while the bites of *T. recurva* are thought to cause only localized reactions (Klotz et al. 2010). Specimens of all these three species have been found infected with *T. cruzi* (Reisenman et al. 2010), and several studies indicate that infection in *T. protracta* and *T. recurva* might be higher than in *T. rubida* (Wood 1949, Bice 1964, Reisenman et al. 2010, Stevens et al. 2012). Female *T. rubida* are potentially very good vectors of *T. cruzi*, as they consistently defecate while feeding (Reisenman et al. 2011) or shortly (<1 min) thereafter (Martínez-Ibarra et al. 2005), whereas immature stages and males do not defecate while feeding (Reisenman et al. 2011). Two small-scale studies suggested that *T. rubida* might be a more efficient vector of *T. cruzi* than *T. protracta*, given its shorter post-feeding defecation delay (Wood 1951, Klotz et al. 2009); the vectorial capacity of *T. recurva* has not been studied. Despite these inter-specific considerations, from an epidemiological point of view, the characteristics of *T. rubida* are the most relevant, because $>95\%$ of the triatomines that reach human dwellings in southern Arizona belong to this species (Fig. 1), 40% of which have been recently reported to be infected with *T. cruzi* (Reisenman et al. 2010). Thus, *T. rubida* has the potential of transmitting *T. cruzi* to humans, although transmission has not been reported to date in Arizona. In the U.S., *T. cruzi* is maintained as a stable zoonosis involving mammalian reservoirs of the parasite (such as packrats, skunks, and raccoons; Wood 1949, Ryckman 1986, Brown et al. 2010) and triatomine insects that live in close association (e.g., in their

nests) with them. Importantly dogs, which are very important in establishing domestic cycles of transmission of *T. cruzi* in Latin America (Gürtler et al. 1991, 2007) and in southern Texas (Beard et al. 2003), have been reported to be infected with *T. cruzi* with an overall prevalence as high as 20.3% in Texas (Kjos et al. 2008b). No such studies have been conducted in Arizona, but seroprevalence should be high, given the large number of pet dogs residing in areas with potential contact with infected insects and wild mammalian hosts of the parasite (Barr et al. 1991a, b). Dogs could also acquire the infection if they chew infected insects (Montenegro et al. 2002, Gürtler et al. 2009).

We found that the onset of the dispersal season is closely related to rising temperatures (Fig. 3; Supp. Fig. 1B [online only]) compatible with insect flight (Lehane et al. 1992, Gurevitz et al. 2006). It appears that both *T. protracta* and *T. recurva* can fly at lower temperatures, as these species dispersed earlier than *T. rubida* in all years (Fig. 4). High evening temperatures and relatively calm air appear to promote *T. rubida* flights, which occurred during the first 4 hr after dark (Ekkens 1981).

In the case of *T. rubida*, we found a similar ratio of females to males in all years (except in 2006, when females were more abundant; Fig. 2). Both sexes followed a roughly similar temporal pattern of dispersal in all years (data not shown), in contrast with a previous report that male *T. rubida* were more common early in the season (Ekkens 1981). It is likely, as reported in previous studies of *T. rubida* (Ekkens 1981) and of other triatomine species (Lehane et al. 1992, Minoli and Lazzari 2006, Carbajal de la Fuente et al. 2007), that starvation is the main driver of dispersal. Most insects collected in our study appeared flat and hungry. For *T. protracta* and *T. recurva*, the sex distribution was quite different. In the case of *T. recurva*, as previously reported (Ekkens 1981), in all years we observed a highly disproportionate ratio of males to females (Fig. 2). That was also the case for *T. protracta*, although fewer insects were collected (Fig. 2). More information about the wild hosts and behavior of *T. recurva* is necessary to interpret these results.

In this study, volunteers were asked to capture insects that were found inside and/or around their houses. While strictly speaking this is not a random sample, the large number of insects (1,878 collected in many nights over 4 yr) obtained from many different collection sites (range: 16–118 per year) likely helped to overcome this sampling problem, which nevertheless should be considered when interpreting our results. Biases might have been introduced if, for instance, sampling effort varied between collectors, nights, and/or different dispersal seasons. Despite these possible biases we observed a remarkably consistency in the species proportions, sex ratios, and the temporal pattern of dispersal throughout the years. The benefit of our collection method, however, is that it allowed us to obtain a large sample (much larger than what our own efforts could have achieved) of insects that are epidemiologically important because they had reached houses. Indeed, 55–60% of the in-

sects were collected inside houses, 30–35% of which were found in or near beds (Fig. 6) and therefore likely to have fed on humans. Some collectors (20–29%) reported having been bitten, which is likely an underestimation, because most bites occur during sleeping. Moreover, a recent report on the bloodmeals of *T. rubida* collected in the area of study indicated that this species feeds on humans (Stevens et al. 2012). In summary, the close association of kissing bugs with human habitations in southern Arizona indicates that the risks for human health, both as cause of severe allergic reactions and as potential vectors of *T. cruzi*, are higher than previously thought.

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References Cited

- Barr, S. C., V. A. Dennis, and T. R. Klei. 1991a. Serologic and blood culture survey of *Trypanosoma cruzi* infection in four canine populations of southern Louisiana. *Am. J. Vet. Res.* 52: 570–573.
- Barr, S. C., S. P. Schmidt, C. C. Brown, and T. R. Klei. 1991b. Pathologic features of dogs inoculated with North American *Trypanosoma cruzi* isolates. *Am. J. Vet. Res.* 52: 2033–2039.
- Barr, S. C. 2009. Canine Chagas' Disease (American Trypanosomiasis) in North America. *Vet. Clin. North Am. Small Anim. Pract.* 39: 1055–1064.
- Barrozo, R. B., and C. R. Lazzari. 2004. The response of the blood-sucking bug *Triatoma infestans* to carbon dioxide and other host odours. *Chem. Senses* 29: 319–329.
- Beard, C. B., G. Pye, F. J. Steurer, R. Rodriguez, R. Campman, A. Townsend Peterson, J. Ramsey, R. A. Wirtz, and L. E. Robinson. 2003. Chagas Disease in a domestic transmission cycle in Southern Texas, USA. *Emerg. Infect. Dis.* 9: 103–105.
- Bern, C., S. Kjos, M. J. Yabsley, and S. P. Montgomery. 2011. *Trypanosoma cruzi* and Chagas' Disease in the United States. *Clin. Microbiol. Rev.* 24: 655–681.
- Bice, D. E. 1964. The incidence of *Trypanosoma cruzi* in *Triatoma* of Tucson, Arizona. M.Sc. thesis, University of Arizona, Tucson, AZ.
- Brown, E. L., D. M. Roellig, M. E. Gompper, R. J. Monello, K. M. Wenning, M. W. Gabriel, and M. J. Yabsley. 2010. Seroprevalence of *Trypanosoma cruzi* among eleven potential reservoir species from six states across the southern United States. *Vector-Borne Zoonot. Dis.* 10: 757–763.
- Cantey, P. T., S. L. Stramer, R. L. Townsend, H. Kamel, K. Ofafa, C. W. Todd, M. Currier, S. Hand, W. Varnado, E. Dotson, C. Hall, P. L. Jett, and S. P. Montgomery. 2012. The United States *Trypanosoma cruzi* infection study: evidence for vector-borne transmission of the parasite that causes Chagas disease among United States blood donors. *Transfusion* (doi:10.1111/j.1537-2995.2012.03581.x).
- Carbajal de la Fuente, A., S. A. Minoli, C. M. Lopes, F. Noireau, C. R. Lazzari, and M. G. Lorenzo. 2007. Flight dispersal of the Chagas disease vectors *Triatoma brasiliensis* and *Triatoma pseudomaculata* in northeastern Brazil. *Acta Trop.* 101: 115–119.
- Curra, C. I., A. M. Mejía-Jaramillo, T. Duffy, J. M. Burgos, M. Rodruigero, M. V. Cardinal, S. Kjos, R. Gurgel-Gonçalves, D. Blanchet, L. M. De Pablos, et al. 2010. *Trypanosoma cruzi* I genotypes in different geographical regions and transmission cycles based on a microsatellite motif of the intergenic spacer of spliced-leader genes. *Int. J. Parasitol.* 40: 1599–1607.
- Dorn, P. L., L. Perniciario, M. J. Yabsley, D. M. Roellig, G. Balsamo, J. Diaz, and D. Wesson. 2007. Autochthonous transmission of *Trypanosoma cruzi*, Louisiana. *Emerg. Infect. Dis.* 13: 605–607.
- Eckens, D. B. 1981. Nocturnal flights of *Triatoma* (Hemiptera: Reduviidae) in Sabino Canyon, Arizona. I. Light collections. *J. Med. Entomol.* 18: 211–227.
- Guerenstein, P. G., and C. R. Lazzari. 2010. The role of olfaction in host seeking of triatomine bugs, pp. 309–325. In T. Knols (ed.), *Ecology and Control of Vector-Borne Diseases Vol. 2: Olfaction in Vector-Host Interactions*. Wageningen Academic, The Netherlands.
- Guerevitz, J. M., L. A. Ceballos, U. Kitron, and R. E. Gürtler. 2006. Flight initiation of *Triatoma infestans* (Hemiptera: Reduviidae) under natural climatic conditions. *J. Med. Entomol.* 43: 143–150.
- Gürtler, R. E., L. A. Ceballos, P. Ordóñez-Krasnowski, L. A. Lanati, R. Stariolo, and U. Kitron. 2009. Strong host-feeding preferences of the vector *Triatoma infestans* modified by vector density: implications for the epidemiology of Chagas Disease. *PLoS Negl. Trop. Dis.* 3: e447. (doi: 10.1371/journal.pntd.0000447).
- Gürtler, R. E., M. C. Cécere, M. A. Lauricella, M. V. Cardinal, U. Kitron, and J. E. Cohen. 2007. Domestic dogs and cats as sources of *Trypanosoma cruzi* infection in rural northwestern Argentina. *Parasitology* 134: 69–82.
- Gürtler, R. E., M. C. Cécere, D. N. Rubel, R. M. Petersen, N. J. Schweigmann, M. A. Lauricella, M. A. Bujas, E. L. Segura, and C. Wisnivesky-Colli. 1991. Chagas disease in north-west Argentina: infected dogs as a risk factor for the domestic transmission of *Trypanosoma cruzi*. *Trans. R. Soc. Trop. Med. Hyg.* 85: 741–745.
- Herwaldt, B. L., M. J. Grijalva, A. L. Newsome, C. R. McGhee, M. R. Powell, D. G. Nemece, F. J. Steurer, and M. L. Eberhard. 2000. Use of polymerase chain reaction to diagnose the fifth reported US case of autochthonous transmission of *Trypanosoma cruzi*, in Tennessee, 1998. *J. Infect. Dis.* 181: 395–399.
- Kjos, S. A., K. F. Snowden, and J. K. Olson. 2008a. Biogeography and *Trypanosoma cruzi* infection prevalence of Chagas Disease vectors in Texas, USA. *Vector-Borne Zoonot. Dis.* 1: 1–10.
- Kjos, S. A., K. F. Snowden, T. M. Craig, B. Lewis, N. Ronald, and J. K. Olson. 2008b. Distribution and characterization of canine Chagas disease in Texas. *Vet. Parasitol.* 152: 249–256.
- Klotz, J. H., P. L. Dorn, J. L. Logan, L. Stevens, J. L. Pinna, J. O. Schmidt, and S. A. Klotz. 2010. "Kissing bugs": potential disease vectors and cause of anaphylaxis. *Clin. Infect. Dis.* 50: 1629–1634.
- Klotz, S. A., P. L. Dorn, J. H. Klotz, J. L. Pinna, C. Weirauch, J. R. Kurtz, and J. Schmidt. 2009. Feeding behavior of triatomines from the southwestern United States: an update on potential risk for transmission of Chagas disease. *Acta Trop.* 111: 114–118.

- Kofoed, C. A., and B. G. Whitaker. 1936. Natural infection of American human trypanosomiasis in two species of cone-nosed bugs, *Triatoma protracta* Uhler and *Triatoma uhleri* Neiva, in the Western United States. *J. Parasitol.* 22: 259–263.
- Lehane, M. J., P. K. McEwen, C. J. Whitaker, and C. J. Schofield. 1992. The role of temperature and nutritional status in flight initiation by *Triatoma infestans*. *Acta Trop.* 52: 27–38.
- Lynch, P. J., and J. L. Pinnas. 1978. “Kissing bug” bites. *Triatoma* species as an important cause of insect bites in the Southwest. *CUTIS* 22: 591.
- Martínez-Ibarra, J. A., B. Noguera-Torres, E. P. González, R. Alejandro-Aguilar, M. Solorio-Cibrián, S. P. Barreto, H. I. Gómez-Estrada, and J. C. Trujillo-García. 2005. Development of *Triatoma rubida* *sonoriana*, *Triatoma barberi*, and *Meccus Mazzottii* (Heteroptera, Reduviidae) under laboratory conditions. *J. Am. Mosquito Control* 21: 310–315.
- Minoli, S. A., and C. R. Lazzari. 2006. Take-off activity and orientation of triatomines (Heteroptera: Reduviidae) in relation to the presence of artificial lights. *Acta Trop.* 97: 324–330.
- Montenegro, V. M., M. Jimenez, J. C. Dias, and R. Zeledón. 2002. Chagas disease in dogs from endemic areas of Costa Rica. *Mem. Inst. Oswaldo Cruz.* 97: 491–494.
- Ochs, D. E., V. S. Hnilica, D. R. Moser, J. H. Smith, and L. V. Kirchoff. 1996. Postmortem diagnosis of autochthonous acute chagasic myocarditis by polymerase chain reaction amplification of a species-specific DNA sequence of *Trypanosoma cruzi*. *Am. J. Trop. Med. Hyg.* 54: 526–529.
- Packchianian, A. 1942. Reservoirs hosts of Chagas’ Disease in the state of Texas. *Am. J. Trop. Med. Hyg.* 22: 623–631.
- Pinnas, J. L., R. E. Lindberg, T. M. W. Chen, and G. C. Meinke. 1986. Studies of kissing-bug sensitive patients: evidence for the lack of cross-reactivity between *Triatoma protracta* and *Triatoma rubida* salivary gland extracts. *J. Allergy Clin. Immunol.* 77: 364–370.
- Pung, O. J., C. W. Banks, D. N. Jones, and M. W. Krissinger. 1995. *Trypanosoma cruzi* in wild raccoons, opossums, and triatomine bugs in southeast Georgia, USA. *J. Parasitol.* 81: 324–326.
- Reisenman, C. E., T. Gregory, P. G. Guerenstein, and J. G. Hildebrand. 2011. Feeding and defecation behavior of *Triatoma rubida* (Uhler, 1894) (Hemiptera: Reduviidae) under laboratory conditions, and its potential role as a vector of Chagas Disease in Arizona, USA. *Am. J. Trop. Med. Hyg.* 85: 648–656.
- Reisenman, C. E., G. Lawrence, P. G. Guerenstein, T. Gregory, E. Dotson, and J. G. Hildebrand. 2010. Infection of kissing bugs with *Trypanosoma cruzi*, Tucson, Arizona, USA. *Emerg. Infect. Dis.* 16: 400–405.
- Rosypal, A. C., R. T. Tidwell, and D. S. Lindsay. 2007. Wild canids are reservoir hosts for *Leishmania infantum* and *Trypanosoma cruzi* from South Carolina. *J. Parasitol.* 93: 955–957.
- Ryckman, R. E. 1986. The vertebrate hosts of the Triatominae of North and Central America and the West Indies (Hemiptera: Reduviidae: Triatominae). *Bull. Soc. Vector Ecol.* 11: 221–241.
- Schiffler, R. J., G. P. Mansur, and T. R. Navin. 1984. Indigenous Chagas’ Disease (American trypanosomiasis) in California. *J. Am. Med. Assoc.* 251: 2983–2984.
- Shadomy, S. V., S. C. Waring, and C. L. Chappell. 2004. Combined use of enzyme-linked immunosorbent assay and flow cytometry to detect antibodies to *Trypanosoma cruzi* in domestic canines in Texas. *Clin. Diagn. Lab. Immunol.* 11: 313–319.
- Stevens, L., P. L. Dorn, J. Hobson, N. M. de la Rua, D. E. Lucero, J. H. Klotz, J. O. Schmidt, and S. A. Klotz. 2012. Vector blood meals and Chagas disease transmission potential, United States. *Emerg. Infect. Dis.* 18: 646–649.
- Wehrle, L. P. 1939. Observations on three species of *Triatoma* (Hemiptera: Reduviidae). *Bull. Brooklyn Entomol. Soc.* 34: 145–154.
- Wood, S. F. 1941. Notes on the distribution and habits of Reduviid vectors of Chagas’ Disease in the Southwest United States. *Pan-Pac. Entomol.* 27: 115–118.
- Wood, S. F. 1942. Observations on vectors of Chagas’ disease in the United States. I. California. *Bull. South. Calif. Acad. Sci.* 41: 61–69.
- Wood, S. F. 1943a. Observations on vectors of Chagas’ Disease in the United States. *Am. J. Trop. Med. Hyg.* 23: 315–320.
- Wood, S. F. 1943b. Observations on vectors of Chagas’ Disease in the United States. II Arizona. *Am. J. Trop. Med. Hyg.* 23: 315–320.
- Wood, S. F. 1949. Additional observations on *Trypanosoma cruzi* Chagas, from Arizona in insects, rodents and experimentally infected animals. *Am. J. Trop. Med. Hyg.* 29: 43–55.
- Wood, S. F. 1950. Dispersal flight of *Triatoma* in southern Arizona. *J. Parasitol.* 36: 498–499.
- Wood, S. F. 1951. Importance of feeding and defecation times of insect vectors in transmission of Chagas’ Disease. *J. Econ. Entomol.* 44: 52–54.
- Wood, S. F. 1957. Conenose bug and trypanosome observations for 1955–56 from southwestern national monuments. *Bull. South. Calif. Acad. Sci.* 56: 51.
- Wood, S. F., and F. D. Wood. 1961. Observations on vectors of Chagas’ Disease in the United States. III. New Mexico. *Am. J. Trop. Med. Hyg.* 10: 155–165.
- Woody, N. C., and H. B. Woody. 1955. American trypanosomiasis (Chagas’s Disease): first indigenous case in the United States. *J. Am. Med. Assoc.* 159: 676–677.
- World Health Organization. 2011. Chagas disease (American Trypanosomiasis). Fact Sheet no. 340. (<http://www.who.int/mediacentre/factsheets/fs340/en/index.html>).
- Yabsley, M. J., and G. Pittman Noblet. 2002. Seroprevalence of *Trypanosoma cruzi* in raccoons from South Carolina and Georgia. *J. Wildl. Dis.* 38: 75–83.
- Zeledón, R., and J. E. Rabinovich. 1981. Chagas’ Disease: an ecological appraisal with special emphasis on its insect vectors. *Annu. Rev. Entomol.* 26: 101–133.

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