



# Phenology and environmental predictors of *Triatoma sanguisuga* dispersal in east-central Texas, United States

Juan P. Fimbres-Macias<sup>a</sup>, Trevor A. Harris<sup>b</sup>, Sarah A. Hamer<sup>a</sup>, Gabriel L. Hamer<sup>c,\*</sup>

<sup>a</sup> Department of Veterinary Integrative Biosciences, Texas A&M University, College Station, TX 77843, USA

<sup>b</sup> Department of Statistics, Texas A&M University, College Station, TX 77843, USA

<sup>c</sup> Department of Entomology, Texas A&M University, College Station, TX 77843, USA

## ARTICLE INFO

### Keywords:

Kissing bug  
Chagas disease  
Dispersal phenology  
Wind-facilitated dispersal

## ABSTRACT

Of 11 triatomine species in the United States (US), *Triatoma sanguisuga* has the widest distribution across a 23-state region encompassing the southeastern US. This species consistently feeds on humans and dogs and has a high infection prevalence with the Chagas parasite *Trypanosoma cruzi*, with over 30–60% of adults infected. Little is known about the phenology and environmental predictors of dispersal activity of *Triatoma sanguisuga*. Using manual searches standardized by effort, we sampled kissing bugs in east central Texas, US every other night from June to November 2020 to determine their phenology and environmental predictors of activity. We found 176 triatomines alive, all of which were *T. sanguisuga*, with peak collections in early August and cessation of activity by late October; the phenology as determined by this active surveillance matched what has been reported using a passive community science approach. Using a negative binomial regression, we found temperature to have a positive correlation with *T. sanguisuga* dispersal activity, while wind speed had a significant negative correlation. We identified increased collections during sampling sessions with precipitation during the preceding 22 h. Further, wind from the southwest - the direction of most of the sylvatic habitat in the study area - was correlated with an increased dispersal activity, suggesting wind-facilitated dispersal. Given concerns for human and animal Chagas disease within the distribution of *T. sanguisuga*, vector control strategies can be adapted based on the factors influencing dispersal behavior.

## 1. Introduction

Chagas disease is a zoonosis caused by the protozoan parasite, *Trypanosoma cruzi*, that infects at least 180 species of mammals including humans, domestic animals (e.g. dogs, cats and livestock) and wild mammals (e.g. rodents, marsupials and armadillos) (Herrera, 2010). For humans the main form of transmission is vector-borne, in which triatomine insects ('kissing bugs') obtain the parasite by feeding on infected animals and then transmit infectious material through feces which contaminates the bite wound or mucous membrane. In addition, oral transmission occurs in humans following ingestion of food contaminated with feces or the triatomine itself (Filigheddu et al., 2017), which also occurs in domestic and wild mammals (de Noya and González, 2015). Chagas disease occurs throughout the world with an estimated 7 million people infected, most of them in the Americas where *T. cruzi* is endemic and results in a large public health burden in Latin America (GBD, 2019).

There are an estimated 288,000 persons infected with *T. cruzi* living in the US, including predominantly imported cases with exposure in other countries (Irish et al., 2022). Autochthonous transmission is reported in the US, although the frequency of human exposure is low, likely due to several factors such as less frequent colonization of human homes by triatomines (Bern and Montgomery, 2009). A recent review found 76 case reports of suspected or confirmed locally acquired human Chagas disease between 2000 and 2018, nearly ten times the case counts of the prior 50 years of scientific literature (Lynn et al., 2020). The majority of the cases originated in Texas with a total of 48 (26 confirmed and 22 suspected) followed by Louisiana with 7 suspected cases (Lynn et al., 2020).

From the 11 species reported in the US, *Triatoma sanguisuga*, colloquially known as the "eastern blood-sucking conenose bug", has the largest geographic distribution with presence across 23 states from Wyoming to the east coast (Bern et al., 2019; Reeves and Miller, 2020; Wozniak et al., 2015). The prevalence of *T. cruzi* infection in

\* Corresponding author.

E-mail address: [ghamer@tamu.edu](mailto:ghamer@tamu.edu) (G.L. Hamer).

<https://doi.org/10.1016/j.actatropica.2023.106862>

Received 20 December 2022; Received in revised form 8 February 2023; Accepted 10 February 2023

Available online 12 February 2023

0001-706X/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).



**Fig. 1.** Map of study area around the administrative building at Texas A&M University where dispersing *T. sanguisuga* was sampled from June to Oct. 2020. The sylvatic habitat with forest and shrubs occurs to the southwest of the sampling location while most other directions are urban landscapes.

*T. sanguisuga* differs across the range of distribution e.g., 60.4% in southeastern Louisiana (Cesa et al., 2011), 40% in Louisiana (Waleckx et al., 2014), 48.8% in Texas (Curtis-Robles et al., 2018a, 2017; Kjos et al., 2009). A quantitative synthesis of triatomine bloodmeal analysis studies in the US found that humans were the second most common blood source in *T. sanguisuga*, preceded only by dogs (Busselman and Hamer, 2022). Furthermore, after collecting kissing bugs at the site of the first autochthonous case of transmission of Chagas in Louisiana, it was found that about 56% of triatomines were infected with *T. cruzi* (Dorn et al., 2007). In a 4-year study using kissing bugs submitted through a community science program, *T. sanguisuga* was the second most common species in Texas, with 421 out of 2831 specimens, preceded by *Triatoma gerstaeckeri* (Curtis-Robles et al., 2018b). Approximately half ( $n = 202$ ) of the *T. sanguisuga* were found indoors, with the remainder in dog kennels and other peridomestic environments.

*Triatoma sanguisuga* is generally not known to colonize homes, and peri-domestic and domestic encounters are thought to result from actively dispersing adults by flight, likely driven by mate and/or blood meal seeking behaviors (Wozniak et al., 2015). Triatomines are also able to disperse by walking (Abraham et al., 2011; Lobbia and Mougabure-Cueto, 2020), although this is likely less frequently the mode of movement when adults arrive to the domestic environment in the Southern US. Sylvatic populations of *T. sanguisuga* have been associated with *Neotoma* spp. nests and also cavities in trees, rocks, or underground (homes of nidicolous mammals such as Virginia opossum; *Didelphis virginiana*, raccoons; *Procyon lotor*, or squirrels; *Sciurus* spp.) (Abad-Franch et al., 2021).

Knowledge of the periods of activity and environmental predictors of dispersal of triatomines could be useful in targeting vector control initiatives and public health messaging to reduce human and animal disease risk. The limited records for *T. sanguisuga* adult flight dispersal phenology comes from a community science program that relies on passive collections by citizens, and is thus not a systematic active sample (Hamer et al., 2018). Artificial light is known to attract nocturnal insects, with mechanisms known as “the light compass theory” (Sotthibandhu and Baker, 1979), disorientation by “dazzling” (Verheijen,

1960), and more (discussed by Owens and Lewis, 2018). This phenomenon includes triatomines (Pacheco-Tucuch et al., 2012), resulting in aggregations of dispersing adults around outdoor lights at night. The objective of the current study was to conduct a longitudinal active surveillance project through the triatomine dispersal season at a focal study site in East Central, Texas to identify abiotic predictors of triatomine activity. Improved understanding of factors influencing adult dispersal will enhance vector control initiatives to limit human and animal Chagas disease.

## 2. Methods

### 2.1. Study area

The study was carried out at an administrative building on the campus of Texas A&M University in College Station, Texas (Fig. 1). This administrative building had a report of a triatomine crawling inside the building in 2016 and specimens were subsequently submitted to the Kissing Bug Community Science Program (Curtis-Robles et al., 2015). The building is surrounded by patchy vegetation to the south and west containing scattered homes, ponds, creeks, and abundant natural vegetation. To the northwest is a two-lane highway followed by the Texas A&M University Veterinary Medical Park which houses different species of livestock such as cattle and goats. The nearest house is approximately 300 m southwest. There is a 25 m paved parking lot between the vegetation and the building. The exterior of the building has 19 lights which are 250 watt metal halid wall pack fixtures that operate on a photo switch, creating the only source of artificial light in a 300 meter radius (Fig. 1).

### 2.2. Standardized triatomine collections

We manually collected kissing bugs every other night for 78 days (sessions) starting on June 4th and ending on November 1st, 2020. The collecting method consisted of walking around the building and searching the walls and ground with flashlights. At all times the collector

**Table 1**

AIC values from the models created during our backwards model selection process evaluating environmental predictors of *Triatoma sanguisuga* dispersal in East-Central Texas.

Model	Variables included	Number of variables	AIC
M1	Temp, WS_cat, hum, ML, cum_precipt, intercardinal, month	7	296.74
M2	Temp, WS, hum, ML, cum_precipt, intercardinal, month	7	292.86
M3	Temp, WS, hum, ML, cum_precipt, intercardinal	6	290.75
M4	Temp, WS, hum, ML, bin_precipt, intercardinal	6	289.05
M5	Temp, WS, ML, bin_precipt, intercardinal	5	288.86
M6	Temp, WS, ML, bin_precipt, N.S.	5	288.42
M7	Temp, WS, ML, bin_precipt, E.W.	5	284.90
M8	Temp, WS, ML, bin_precipt, cardinal	5	284.62
M9	Temp, WS, ML, bin_precipt, SW_w	5	283.49
M10	Temp, WS, moon_binary, bin_precipt, SW_w	5	282.33
M11	Temp, WS, bin_precipt, SW_w	4	282.31
M12	Temp, WS, moon_lit, bin_precipt, SW.	5	280.91

Temp= temperature●; WS\_cat= wind speed categorized◇; hum= humidity●; ML= average moonlight●; cum\_precipt= cumulative precipitation●; intercardinal = wind direction (NE, SE, SW, NE)◇; month◇; bin\_precipitation= if it rained during the sampling day■; N.S.= wind categorized only as N and S◇; E.W.= wind categorized only as E and W◇; SW\_w = if wind was blowing from SW■; moon\_binary= if moon was visible over horizon during the session■; moon\_lit= percentage of moon illuminated●.

- : continuous variable.
- ◇: factor variable.
- : binary variable.

was walking slowly (≈3.5 km/h) and stopping only when a triatomine or suspected triatomine insect was spotted. Triatomines high on the building wall were captured with a plastic bag connected to a telescopic paint pole. The paved parking lot, sidewalk, and building wall was light in color, facilitating the ability to detect triatomines. The session began at sunset, lasted two hours, and was divided in periods of 20 min (six periods per session). The collectors circumnavigated the entire building approximately 1.5 times each period. An author (JPFM) was present for all 78 sessions with 64 performed individually, 11 were performed with two observers, 2 were performed with three observers, and 1 was performed with 4 observers. We used a black light with a white blanket as an attractant from session 6 to 12 (June 11 to July 15) located on the wall facing southwest (Fig. 1), but stopped given the limited success of it for attracting triatomines compared to the artificial lights on the building. All the specimens were taken to the laboratory to determine

species and sex using a dichotomous key (Lent and Wygodzinsky, 1979). All live specimens were deposited in our triatomine colony for future research projects.

We retrieved weather data from a Texas A&M AgriLife Extension weather station located 1.2 km north from our study site (TexasET Network, 2020), including: temperature (°C), wind speed (km/h), minimum relative humidity (%), wind direction, and cumulative precipitation (cm). We calculated the average wind direction for the two hours period according to (The Meteorological Resource Center, 2020). We used data from a website to determine visibility of the moon in College Station, TX, during the sessions (Time and Date, 2020) to create the variable “moon\_binary”. To know the percentage of moon illuminated we used data from an online almanac (Moon Phases Calendar,

**Table 2**

Estimates, CI and p-value for the best fit model (M12) of environmental predictors of *Triatoma sanguisuga* dispersal in East-Central Texas.

	Estimate (Log-Count)	95% Confidence interval	p-Value
(Intercept)	-2.06	-4.05, -0.22	0.033
temperature	0.10	0.04, 0.17	0.002
wind speed	-0.11	-0.15, -0.06	<0.001
moon_lit	-0.54	-1.11, 0.03	0.073
bin_precip	0.51	0.02, 0.99	0.041
SW_wind	0.62	0.14, 1.10	0.011

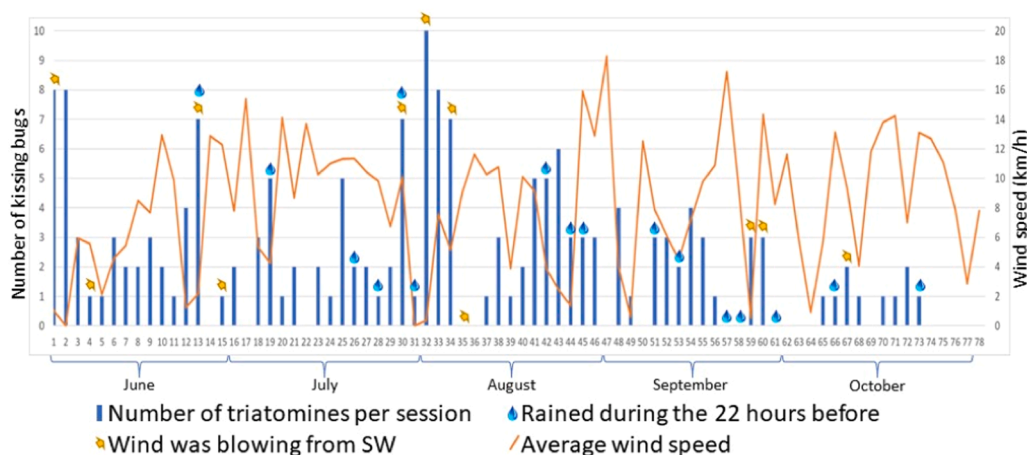
Covariates: **temperature** (degrees Celsius), **wind speed** (average wind speed during the session, km/h), **moon\_lit** (percentage of moon illuminated), **bin\_precip** (if it rained during the 22 h before sampling), **SW\_wind** (if wind was blowing from SW).

**Table 3**

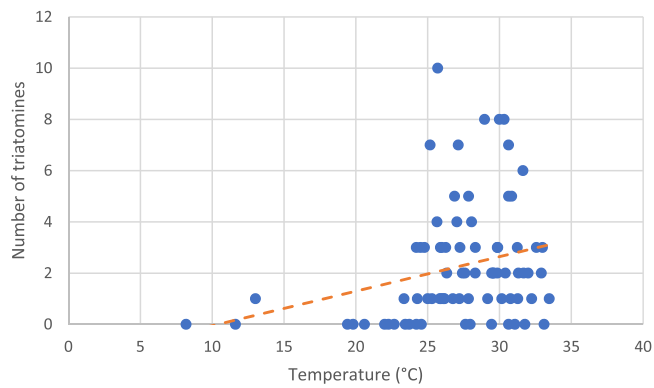
Number of sessions with wind from each intercardinal direction, number of triatomines and proportion.

Wind direction	Number of sessions	Number of triatomines	Proportion of triatomines per session with wind in that direction
NE	21	36	1.47
NW	5	4	0.8
SE	39	78	2.0
SW	11	49	4.45
No wind	2	9	4.5

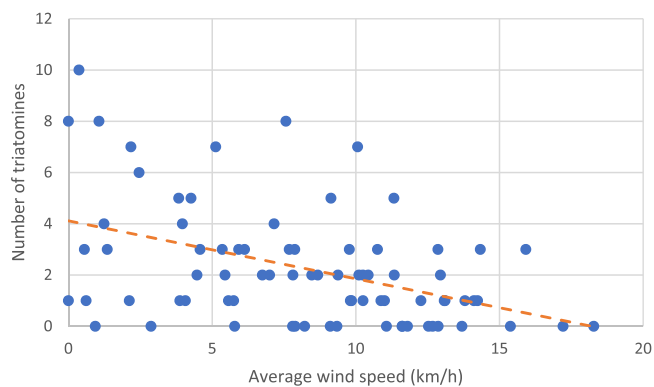
NE= wind from northeast.  
 NW= wind from northwest.  
 SE= wind from southeast.  
 SW= wind from southwest.  
 No wind = the windspeed average was 0 km/h for that session.



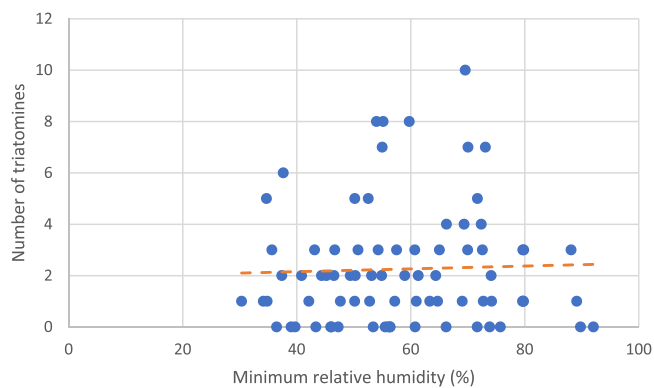
**Fig. 2.** Number of *Triatoma sanguisuga* found during each session and values for the most important predictors of activity in east-central Texas between June and November 2020.



**Fig. B.1.** Scatter plot of the number of triatomines found and the average temperature of each session.



**Fig. B.2.** Scatter plot of the number of triatomines and the average wind speed (km/h) of each session.

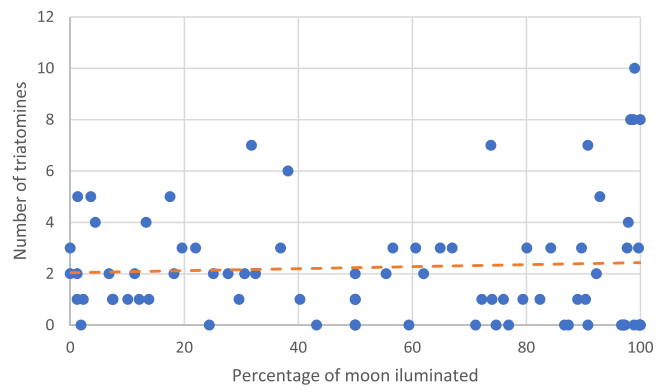


**Fig. B.3.** Scatter plot of the number of triatomines and the average minimum relative humidity of each session (%).

2020), and created the variable “moon\_lit”. We retrieved cloud coverage percentage using The Weather Channel mobile application for each session (The Weather Channel, 2020). We then created a complex variable called “average moonlight” composed of three factors (moon\_binary (1–0)\*moon\_lit(%)\*cloud coverage(%).

**2.3. Statistical analysis**

We considered all the triatomines seen during a two-hour session as the outcome variable and interpreted as recently dispersed adults that arrived to the building by flight as attracted to the lights. We estimated a negative binomial regression to account for overdispersion using R



**Fig. B.4.** Scatter plot of the number of triatomines and the percentage of moon illuminated of each session.

version 4.1.1 in package MASS (R Core Team, 2021). We used the person hours of each session as an offset (accounting for the sessions when there was more than one observer). Model variables included average temperature (°C) of the two hours sampling period (for the rest of variables, when we refer to average it indicates the average of the two hours sampling period), average wind speed categorized (0–6; 7–12; 13–18 km/h), average wind speed continuous, average minimum relative humidity (%), average moonlight (ranging from 0 to 1), moon binary (if it was visible over horizon during the session), percentage of moon illuminated (disregarding cloud and visibility), cumulative precipitation, precipitation as binary (if it rained the 22 h previous to the sampling session), average wind direction as cardinal (N,E,S,W); as intercardinal (NE, SE, SW, NW); as N and S; as E and W; and as SW-wind binary, and month.

**2.4. Model selection process**

We used a model selection process based on AIC values trying to find the smallest set of predictor variables that would explain our data from a larger pool of variables. We started with factors previously found to be associated with triatomine dispersal activity including temperature and other climatic variables. The first model (M1) included: average temperature, average wind speed categorized, average humidity, average moonlight, cumulative precipitation, intercardinal wind directions, and month. Using an iterative process based on AIC values, we evaluated the predictors in their different forms sometimes replacing them, resulting in 11 models to compare (Table 1). For instance, based on the preliminary data and models suggesting increase in the log-counts of triatomines when wind blew from south and west, we created the variable SW-binary. In a similar way we noticed humidity did not explained our data well, but replacing it with rain in the prior 22 h as binary variable improved the model (see Appendix A for detailed explanation of the model selection process).

**3. Results**

The total number of person hours while searching for triatomines was 185.5 during 78 sessions, the average distance walked by a single observer was 5 km per session as the building was circumnavigated. A total of 182 triatomines were collected- all were identified as *T. sanguisuga*- averaging 2.3 per session (± 5.4), and ranging from 0 to 10. All specimens were adults and six were found dead (4 F: 2 M), one appeared desiccated, the remaining appeared fresh and likely recently died. All of the live specimens appeared to be starved, as judged by personnel experienced with blood feeding triatomines in laboratory settings. We used 176 insects that were captured alive in the negative binomial regression; (female: male ratio was 1.6: 1), of which 150 (85%) were seen on a wall, 21 (12%) on the ground, three (2%) flying, and two

(1%) near the black light. Most triatomines ( $\approx 70\%$ ) were found on the back of the building, specifically the wall that is facing southwest. From the 176 bugs, 84 (47.7%) were found during the first two temporal periods of the sampling (up to 40 min after sunset), 54 (30.7%) during the 3rd and 4th periods (between 41 and 80 min after sunset), and the remaining 38 (21.6%) during the 5th and 6th periods (between 81 and 120 min after sunset). The monthly kissing bug dispersal activity from largest to smallest was as follows (number of triatomines; triatomines per person hour) August (57; 1.5), June (46; 1.1), July (36; 0.9), September (30; 1.0), and October (10; 0.3). We stopped sampling on November 1st, after five consecutive zero-counts (Fig. 2).

The average wind speed for the two hours of each session was 8.2 km/h and ranged between 0 and 18.3 km/h. The average temperature was 27.1 °C and ranged between 8.2 and 33.5 °C. The average minimum humidity was 58.5% and ranged between 30.4% and 92.1%. It rained 16 times during the days we sampled (considering 22 h before the sampling session), and the cumulative precipitation for those days was 4.1 cm. The lowest and highest temperature with a kissing bug record was 13 and 33 °C; the lowest and highest wind speed was 0 and 16 km/h.

Our final model (M12) included temperature, wind speed, percentage of moon illuminated, precipitation as binary (if it rained or not during the 22 h previous to the sampling session) and, if wind was blowing from southwest as binary (AIC = 280.91) (Table 1). Coefficient estimates are presented for the selected model, CI: 95% and  $p$ -value (Table 2).

Temperature was associated with an increased *T. sanguisuga* dispersal; for each one-unit increase in °C the expected log-count (per person hour) of the number of kissing bugs increased by 0.10 ( $p = 0.002$ ) (Table 2; Fig. B.1). Wind speed had a negative association with *T. sanguisuga* dispersal ( $-0.11, p < 0.001$ , Table 2; Fig. B.2). Percentage of moon illuminated had a marginal negative association with *T. sanguisuga* dispersal  $-0.54$  ( $p = 0.073$ ; Fig. B.4). We found an association of an increase in the expected log-count by 0.51 ( $p = 0.041$ ) if it rained during the 22 h before our sampling session. Sessions with southwest wind had a higher proportion of triatomines relative to the proportion found with the other directions (Table 3), and were associated with an increase in the expected log-count by 0.62 ( $p = 0.011$ ) (Table 2).

#### 4. Discussion

We characterized the phenology and abiotic predictors of dispersal activity for *Triatoma sanguisuga*, the most important vector of the Chagas disease parasite in the eastern US. We documented activity of adult triatomines across nearly the full study period, peaking the first week of August and with diminished activity by the end of October. Notably, the phenology as determined by this active surveillance matched what has been reported using a passive community science approach in which members of the public submitted triatomines they encountered over a 4 years period (Curtis-Robles et al., 2018b), suggesting that data from human encounters reflect dispersal activity of adult triatomines. Almost 65% of the triatomine detections occurred during the first hour after sunset, this pattern has also been observed during studies using light traps (Vazquez-Prokopec et al., 2004). However, triatomines encountered early in the night may have been present at the building following a dispersal event the prior night. We found approximately 1.02 bugs per person hour, this is lower compared to a different Texas study that had an average of 3.8 bugs per hour of manual collection effort (Curtis-Robles et al., 2018b). If we consider only the peak period of activity considering the first three sessions of August, an average of 1.98 bugs per person hour were collected. We found a sex bias towards females with 62%, which is similar to what was reported analyzing almost 500 specimens of *T. sanguisuga* submitted through a community science program for which 60.7% were females (Curtis-Robles et al., 2018a). Contrasting with what was found in southeastern Louisiana where 45.4% out of 293 collected *T. sanguisuga* were females (Cesa et al.,

2011).

Nutritional (Lehane et al., 1992; Lobbia and Mougabure-Cueto, 2020) and reproductive status (McEwen and Lehane, 1994), as well as population density (McEwen et al., 1993), are suggested factors that modulate dispersal behavior in triatomines. All of the specimens we found appeared starved, which matches the predictions that the proportion of poorly fed triatomines dispersing by flight is higher (Lehane et al., 1992). Abiotic environmental conditions as temperature, wind speed, and relative humidity could be key factors for flight initiation (Catala et al., 2017; Vazquez-Prokopec et al., 2006). Furthermore, changes in land cover and occurrence of associated hosts could modulate dispersal behavior of triatomines (Grijalva et al., 2014). We found increased dispersal of triatomines with increasing temperature; this is consistent with an increased activity during warm months as reported by past studies (Di Iorio and Gürtler, 2017; Ekkens, 1981; Lehane et al., 1992; Sjogren and Ryckman, 1966; Vazquez-Prokopec et al., 2006). Among climatic factors that influence the occurrence of triatomines in west-central Brazil, temperature was the predictor that best explained adult dispersal (Pereira et al., 2013). Furthermore, a previous study projecting the distribution of *T. sanguisuga* under climate change scenarios found annual mean temperature to be the variable with the most contribution to its distribution and predicted a shift towards north and south from its current range (Garza et al., 2014).

The negative effect of wind speed on the flight dispersal has also been observed in other triatomines including *Triatoma infestans* (Vazquez-Prokopec et al., 2006); *T. protracta* (Sjogren and Ryckman, 1966) and *T. rubida* (when wind speed exceeded 14 km/h) (Schmidt et al., 2022). We attempted categorization of wind speed because it has been suggested that some air movement encourage some species to fly such as *Triatoma recurva* (Ekkens, 1981), perhaps related to seeking hosts (Barrozo et al., 2017), but this did not improve the model fit.

It has been long known that moonlight has an effect on the number of captures of some insects attracted to light such as noctuid moths (Lepidoptera: Noctuidae) when using light traps (Williams, 1936). For these reasons, the effect of the moon has been explored in different ways as a predictor of triatomine dispersal, including binary (in the horizon or not), percentage illuminated, and moon light visible which considers cloud coverage, in most cases not finding a correlation (Ekkens, 1981; Vazquez-Prokopec et al., 2006). A recent Arizona study found moon presence over the horizon during the sampling (regardless of percentage illuminated or cloud coverage) to be correlated with an increased dispersal of kissing bugs, however they suspected this was an artifact of timing of the season and lunar cycle (Schmidt et al., 2022). We explored moon as a predictor in multiple dimensions and most did not explain variation in *T. sanguisuga* dispersal. Only percentage of moon illuminated (regardless of visibility over the horizon or cloud coverage) was negatively associated with *T. sanguisuga* dispersal and of marginal significance. A relationship with percentage of moon illuminated could be due to antagonism between artificial light and ambient light, as it was suggested for noctuid moths. In this research the authors found that moon fullness decreased the numbers of moths caught in light traps, but did not affect the capture success of baited traps (Yela and Holyoak, 1997). Future studies will be needed to strengthen the understanding of the relationship between moon and triatomine dispersal activity.

Humidity has previously been found to be a weak predictor of triatomine dispersal. For example, (Schmidt et al., 2022) found a small negative effect of humidity on *T. rubida* and *T. protracta*. We found that higher relative humidity increased the expected log-counts of encountering triatomines, but it was highly collinear with other variables and consistently increased the AIC value. For this reason, we replaced humidity with a binary indicator of rain (i.e., if it rained in the prior 22 h or not) which improved the model fit. Our best-fit model suggests that rain in the prior day increased the expected-log count of the number of triatomines by 0.51. Some triatomine species have been found to be more resistant to desiccation due to waterproofing properties of their cuticle (de la Vega and Schilman, 2017; Dulbecco et al., 2020). We are not

aware of any research regarding desiccation tolerance for *T. sanguisuga*, but dispersing after rain events could be a strategy to decrease risk of desiccation upon arrival to a new microhabitat. Alternatively, vertebrates hosts commonly become more active following rain (Brown, 2013), which could increase opportunities for finding a host (Stokes et al., 2001).

Past studies evaluating the influence of wind direction on triatomine dispersal did not find significant associations (Ekkens, 1981; Sjogren and Ryckman, 1966). In the current study, we recovered a higher proportion of triatomines when wind blew from SW than from any other direction (Table 3) and the expected log-count was significantly increased. We attribute this observation to the landscape context around the building in which most of the natural area occurred SW of the study area while areas to the N, E, and SE are mostly urban and less likely to have sylvatic triatomines. To further support this observation that origins of dispersing triatomines came from the SW, we found about 70% of all live adult *T. sanguisuga* along the SW side of the building, despite monitoring the circumference of the building. The collection location on the boundary of city limits allows a unique opportunity to provide evidence of the sylvatic origins of wild kissing bugs. Triatomines originating from the sylvatic habitat to the SW would be attracted to the lights and arrive on the SW side of the building (Fig. 1). Additionally, wind-facilitated dispersal is common in other insects, including arthropod vectors (Fitzgibbon et al., 2019), but we are not aware of past studies suggesting adult kissing bug dispersal is facilitated by wind.

Study limitations include sampling every other night which does not allow us to discern if triatomines could have arrived the current or a previous night. Future studies could include a capture-mark-release-recapture (CMRR) methodology to account for this (Dantas et al., 2022). Furthermore, the use of kill traps could also eliminate the uncertainty of not knowing when the specimen dispersed and the bias of failing to see some individuals (Updyke and Allan, 2018). The effect of the moon on triatomine behavior may be masked by the presence of artificial light at the study site. Further, we did not explore how variation in other cues (e.g., pheromones (Bohman et al., 2018), heat or CO<sub>2</sub> (Barrozo et al., 2017) may have impacted insect behavior. Finally, the earliest collection sessions in June had high numbers of triatomines collected so we may have missed early season dispersal events (Fig. 2).

## 5. Conclusions

Using active sampling, this study details the dispersal of adult *T. sanguisuga* from June to October in east-central Texas with a peak in August. We document several environmental variables predicting

## Appendix A. Model selection description

Model selection process: (AIC values for each model are presented in Table 1). The starting model (M1) included: temperature, wind speed categorized, humidity, moon light, cumulative precipitation, intercardinal wind directions, and month. We started with these variables as past studies have suggested they influence dispersal of insects and to avoid collinearity with other variables. For the second model (M2) we replaced wind speed categorized per wind speed as continuous since it showed a linear outcome, this improved our model fit. Next, we discarded month (M3) since the estimates reflected the kissing bugs per person/hours and it likely was correlated with other variables with seasonality such as temperature and humidity, creating instability in the model. The estimate for cumulative precipitation had the largest standard error, so we replaced it with precipitation as a binary variable (M4). This resulted in humidity to become not significant, but due to concerns with collinearity, we dropped this variable which improved the model fit and made binary precipitation the significant predictor with the highest estimate (M5). All the estimates for the intercardinal wind directions had large errors, but we noticed different patterns emerging for north vs south winds, and east vs west. We replaced wind direction categorizing them only as north and south winds, this improved the model fit and while not significant this suggested a higher estimate for south winds (M6). Next, we categorized winds only as east and west, this improved the model fit and while not significant it suggested a higher estimate for west winds (M7). Then we explored wind direction using the 4 main cardinal directions (N, E, S, W), this improved the model and significantly associated west winds with an increase in the expected log-counts (we point out that there was only one session with west winds using this categorization) (M8). Based on the previous patterns we created a binary variable for southwest winds, this improved the model fit and its estimate was borderline significant ( $p = 0.06$ ) suggesting an increase in the expected log-counts of kissing bugs (M9). At this point moon light was not significant, so we replaced it with a binary variable considering if it was visible over the horizon at the time of sampling, this improved our model but remained not significant (M10). Then we dropped moon which improved our model leaving us only with significant predictors (M11). Lastly, we

*T. sanguisuga* dispersal including higher temperature, lower wind speed, rain in the preceding 22 h, and percentage of moon illuminated. We found that wind blowing from the direction of the majority of forested and scrub habitat increased captured *T. sanguisuga*, suggesting wind-facilitated dispersal. These observations improve the opportunity for future predictive models to be used for identifying nights with higher risk for triatomine dispersal. This study helps to identify when and where dispersing adult kissing bugs will be found which is necessary to help minimize Chagas disease risk in humans and domestic animals.

Automatic citation updates are disabled. To see the bibliography, click Refresh in the Zotero tab.

## Funding

This research was supported by AgriLife Research; NIH R21 5R21AI166446; VMBS Graduate Diversity Fellowship.

## CRediT authorship contribution statement

**Juan P. Fimbres-Macias:** Conceptualization, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Trevor A. Harris:** Conceptualization, Methodology, Formal analysis. **Sarah A. Hamer:** Conceptualization, Resources, Writing – review & editing, Supervision, Project administration. **Gabriel L. Hamer:** Conceptualization, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

## Acknowledgments

We thank Italo Zecca, Jordan Solomon, Meredith Anderson, Keswick Killets, Oskar Hamer, Tabitha Hamer, Johanna Hamer, and Viktor Hamer for assisting with triatomine collections.

explored percentage of moon illuminated, disregarding if it was visible over horizon during the session or cloud coverage, this yielded a borderline significant estimate and slightly improved the model fit (M12).

Model	Variables included	Number of variables	AIC
M1	Temp, WS_cat, hum, ML, cum_precipt, intercardinal, month	7	296.74
M2	Temp, WS, hum, ML, cum_precipt, intercardinal, month	7	292.86
M3	Temp, WS, hum, ML, cum_precipt, intercardinal	6	290.75
M4	Temp, WS, hum, ML, bin_precipt, intercardinal	6	289.05
M5	Temp, WS, ML, bin_precipt, intercardinal	5	288.86
M6	Temp, WS, ML, bin_precipt, N.S.	5	288.42
M7	Temp, WS, ML, bin_precipt, E.W.	5	284.90
M8	Temp, WS, ML, bin_precipt, cardinal	5	284.62
M9	Temp, WS, ML, bin_precipt, SW.	5	283.49
M10	Temp, WS, moon_binary, bin_precipt, SW_w	5	282.33
M11	Temp, WS, bin_precipt, SW.	4	282.31
M12	Temp, WS, moon_lit, bin_precipt, SW_w	5	280.91

Temp= temperature•; WS\_cat= wind speed categorized◊; hum= humidity•; ML= average moonlight•; cum\_precipt= cumulative precipitation•; intercardinal = wind direction (NE, SE, SW, NE)◊; month◊; bin precipitation= if it rained during the sampling day■; N.S.= wind categorized only as N and S◊; E.W.= wind categorized only as E and W◊; SW\_w = if wind was blowing from SW■; moon\_binary= if moon was visible over horizon during the session■; moon\_lit= percentage of moon illuminated•.

•: continuous variable.

◊: factor variable.

■: binary variable.

## Appendix B. Scatterplots of predictor variables with the number of *Triatoma sanguisuga* collected per session

## References

- Abad-Franch, F., Gurgel-Gonçalves, R., Guarneri, A., Lorenzo, M., 2021. The ecology and natural history of wild *Triatominae* in the Americas. In: *Triatominae-The Biology of Chagas disease Vectors*, 5. Springer, pp. 388–431.
- Abraham, L.B., Gorla, D.E., Catalá, S.S., 2011. Dispersal of *Triatoma infestans* and other *Triatominae* species in the arid Chaco of Argentina: flying, walking or passive carriage? The importance of walking females. *Mem. Inst. Oswaldo Cruz* 106 (2), 232–239. <https://doi.org/10.1590/S0074-02762011000200019>.
- Barrozo, R.B., Reisenman, C.E., Guerenstein, P., Lazzari, C.R., Lorenzo, M.G., 2017. An inside look at the sensory biology of triatomines. *J. Insect Physiol.* 97, 3–19. <https://doi.org/10.1016/j.jinsphys.2016.11.003>.
- Bern, C., Messenger, L.A., Whitman, J.D., Maguire, J.H., 2019. Chagas disease in the United States: a public health approach. *Clin. Microbiol. Rev.* 33 (1), e00023. <https://doi.org/10.1128/CMR.00023-19>.
- Bern, C., Montgomery, S.P., 2009. An estimate of the burden of Chagas disease in the United States. *Clin. Infect. Dis.* 49 (5), e52–e54. <https://doi.org/10.1086/605091>. : *An Official Publication of the Infectious Diseases Society of America*.
- Bohman, B., Weinstein, A.M., Unelius, C.R., Lorenzo, M.G., 2018. Attraction of *Rhodnius prolixus* males to a synthetic female-pheromone blend. *Parasit. Vectors* 11 (1), 418. <https://doi.org/10.1186/s13071-018-2997-z>.
- Brown, D.J., 2013. Predictive models for calling and movement activity of the endangered Houston toad. *Am. Midl. Nat.* 169 (2), 303–321. <https://doi.org/10.1674/0003-0031-169.2.303>.
- Busselman, R.E., Hamer, S.A., 2022. Chagas disease ecology in the United States: recent advances in understanding *Trypanosoma cruzi* transmission among triatomines, wildlife, and domestic animals and a quantitative synthesis of vector-host interactions. *Annu. Rev. Anim. Biosci.* 10, 325–348. <https://doi.org/10.1146/annurev-animal-013120-043949>.
- Catala, S.S., Noireau, F., Dujardin, J.P., 2017. Biology of *Triatominae*. *American Trypanosomiasis Chagas disease: One undred Years of Research*, 2nd ed. Elsevier, pp. 145–167.
- Cesa, K., Caillouët, K.A., Dorn, P.L., Wesson, D.M., 2011. High *Trypanosoma cruzi* (Kinetoplastida: trypanosomatidae) prevalence in *Triatoma sanguisuga* (Hemiptera: reduviidae) in Southeastern Louisiana. *J. Med. Entomol.* 48 (5), 1091–1094. <https://doi.org/10.1603/ME10195>.
- Curtis-Robles, R., Auckland, L.D., Snowden, K.F., Hamer, G.L., Hamer, S.A., 2018a. Analysis of over 1500 triatomine vectors from across the US, predominantly Texas, for *Trypanosoma cruzi* infection and discrete typing units. *Infect. Genet. Evol.* 58, 171–180. <https://doi.org/10.1016/j.meegid.2017.12.016>. : *Journal of Molecular Epidemiology and Evolutionary Genetics in Infectious Diseases*.
- Curtis-Robles, R., Hamer, S.A., Lane, S., Levy, M.Z., Hamer, G.L., 2018b. Bionomics and spatial distribution of triatomine vectors of *Trypanosoma cruzi* in Texas and other Southern States, USA. *Am. J. Trop. Med. Hyg.* 98 (1), 113–121. <https://doi.org/10.4269/ajtmh.17-0526>.
- Curtis-Robles, R., Wozniak, E.J., Auckland, L.D., Hamer, G.L., Hamer, S.A., 2015. Combining public health education and disease ecology research: using citizen science to assess chagas disease entomological risk in Texas. *PLoS Negl. Trop. Dis.* 9 (12), e0004235. <https://doi.org/10.1371/journal.pntd.0004235>.
- Curtis-Robles, R., Zecca, I.B., Roman-Cruz, V., Carbajal, E.S., Auckland, L.D., Flores, I., Millard, A.V., Hamer, S.A., 2017. *Trypanosoma cruzi* (Agent of Chagas Disease) in sympatric human and dog populations in “Colonias” of the Lower Rio Grande Valley of Texas. *Am. J. Trop. Med. Hyg.* 96 (4), 805–814. <https://doi.org/10.4269/ajtmh.16-0789>.
- Dantas, E.S., Gurgel-Gonçalves, R., Maciel-de-Freitas, R., Monteiro, F.A., 2022. Simultaneous external and internal marking of *Triatoma sordida* nymphs: trace element efficacy and microgeographic dispersal in a peridomestic Brazilian Cerrado rural household. *Parasit. Vectors* 15 (1), 325. <https://doi.org/10.1186/s13071-022-05451-z>.
- de la Vega, G.J., Schilman, P.E., 2017. Using eco-physiological traits to understand the realized niche: the role of desiccation tolerance in Chagas disease vectors. *Oecologia* 185 (4), 607–618. <https://doi.org/10.1007/s00442-017-3986-1>.
- de Noya, B.A., González, O.N., 2015. An ecological overview on the factors that drives to *Trypanosoma cruzi* oral transmission. *Acta Trop.* 151, 94–102. <https://doi.org/10.1016/j.actatropica.2015.06.004>.
- Di Iorio, O., Gürtler, R.E., 2017. Seasonality and temperature-dependent flight dispersal of *Triatoma infestans* (Hemiptera: reduviidae) and other vectors of Chagas disease in Western Argentina. *J. Med. Entomol.* 54 (5), 1285–1292. <https://doi.org/10.1093/jme/tjx109>.
- Dorn, P.L., Perniciario, L., Yabsley, M.J., Roellig, D.M., Balsamo, G., Diaz, J., Wesson, D., 2007. Autochthonous transmission of *Trypanosoma cruzi*, Louisiana. *Emerg. Infect. Dis.* 13 (4), 605–607. <https://doi.org/10.3201/eid1304.061002>.
- Dulbecco, A.B., Moriconi, D.E., Lynn, S., McCarthy, A., Juárez, M.P., Girotti, J.R., Calderón-Fernández, G.M., 2020. Deciphering the role of *Rhodnius prolixus* CYP4G genes in straight and methyl-branched hydrocarbon formation and in desiccation tolerance. *Insect Mol. Biol.* 29 (5), 431–443. <https://doi.org/10.1111/imb.12653>.
- Ekkens, D.B., 1981. Nocturnal flights of *Triatoma* (Hemiptera: reduviidae) in Sabino Canyon, Arizona: I. Light collections. *J. Med. Entomol.* 18 (3), 211–227. <https://doi.org/10.1093/jmedent/18.3.211>.
- Filigheddu, M.T., Górgolas, M., Ramos, J.M., 2017. Orally-transmitted Chagas disease. *Med. Clínica* 148 (3), 125–131. <https://doi.org/10.1016/j.medcle.2017.02.007> (English Edition).
- Fitzgibbon, W.E., Morgan, J.J., Webb, G.F., Wu, Y., 2019. Spatial models of vector-host epidemics with directed movement of vectors over long distances. *Math. Biosci.* 312, 77–87. <https://doi.org/10.1016/j.mbs.2019.04.003>.
- Garza, M., Arroyo, T.P.F., Casillas, E.A., Sanchez-Cordero, V., Rivaldi, C.-L., Sarkar, S., 2014. Projected future distributions of vectors of *Trypanosoma cruzi* in North America under climate change scenarios. *PLoS Negl. Trop. Dis.* 8 (5), e2818. <https://doi.org/10.1371/journal.pntd.0002818>.
- GBD. (2019). *Prevalence of Chagas diseases estimates*. <https://vizhub.healthdata.org/gbd-results/>.
- Grijalva, M.J., Terán, D., Dangles, O., 2014. Dynamics of sylvatic Chagas disease vectors in Coastal Ecuador is driven by changes in land cover. *PLoS Negl. Trop. Dis.* 8 (6), e2960. <https://doi.org/10.1371/journal.pntd.0002960>.

- Hamer, S.A., Curtis-Robles, R., Hamer, G.L., 2018. Contributions of citizen scientists to arthropod vector data in the age of digital epidemiology. *Curr. Opin. Insect Sci.* 28, 98–104. <https://doi.org/10.1016/j.cois.2018.05.005>.
- Herrera, L., 2010. Una revisión sobre reservorios de *Trypanosoma (Schizotrypanum) cruzi* (Chagas, 1909), agente etiológico de la enfermedad de Chagas. *Bol. Malarial. Salud Ambient.* 50 (1), 3–15.
- Irish, A., Whitman, J.D., Clark, E.H., Marcus, R., Bern, C., 2022. Updated estimates and mapping for prevalence of Chagas disease among adults, United States. *Emerg. Infect. Dis.* 28 (7), 1313–1320. <https://doi.org/10.3201/eid2807.212221>.
- Kjos, S.A., Snowden, K.F., Olson, J.K., 2009. Biogeography and *Trypanosoma cruzi* infection prevalence of Chagas disease vectors in Texas, USA. *Vector Borne Zoonotic Dis.* 9 (1), 41–50. <https://doi.org/10.1089/vbz.2008.0026>.
- Lehane, M.J., McEwen, P.K., Whitaker, C.J., Schofield, C.J., 1992. The role of temperature and nutritional status in flight initiation by *Triatoma infestans*. *Acta Trop.* 52 (1), 27–38. [https://doi.org/10.1016/0001-706x\(92\)90004-h](https://doi.org/10.1016/0001-706x(92)90004-h).
- Lent, H., Wygodzinsky, P.W., 1979. Revision of the Triatominae (Hemiptera, Reduviidae), and their significance as vectors of Chagas' disease. *Bull. AMNH* 163 (3). *v.article*. <https://digitallibrary.amnh.org/handle/2246/1282>.
- Lobbia, P.A., Mougabure-Cueto, G., 2020. Active dispersal in *Triatoma infestans* (Klug, 1834) (Hemiptera: reduviidae: triatominae): effects of nutritional status, the presence of a food source and the toxicological phenotype. *Acta Trop.* 204, 105345 <https://doi.org/10.1016/j.actatropica.2020.105345>.
- Lynn, M.K., Bossak, B.H., Sandifer, P.A., Watson, A., Nolan, M.S., 2020. Contemporary autochthonous human Chagas disease in the USA. *Acta Trop.* 205, 105361 <https://doi.org/10.1016/j.actatropica.2020.105361>.
- McEwen, P.K., Lehane, M.J., 1994. Relationships between flight initiation and oviposition in *Triatoma infestans* (Klug) (Hem., Reduviidae). *J. Appl. Entomol.* 117 (1–5), 217–223. <https://doi.org/10.1111/j.1439-0418.1994.tb00728.x>.
- McEwen, P.K., Lehane, M.J., Whitaker, C.J., 1993. The effect of adult population density on flight initiation in *Triatoma infestans* (Klug) (Hem., Reduviidae). *J. Appl. Entomol.* 116 (1–5), 321–325. <https://doi.org/10.1111/j.1439-0418.1993.tb01203.x>.
- Moon Phases Calendar*. (2020). <https://www.almanac.com/astronomy/moon/calendar>.
- Owens, A.C.S., Lewis, S.M., 2018. The impact of artificial light at night on nocturnal insects: a review and synthesis. *Ecol. Evol.* 8 (22), 11337–11358. <https://doi.org/10.1002/ece3.4557>.
- Pacheco-Tucuch, F.S., Ramirez-Sierra, M.J., Gourbière, S., Dumonteil, E., 2012. Public street lights increase house infestation by the Chagas disease vector *Triatoma dimidiata*. *PLoS ONE* 7 (4), e36207. <https://doi.org/10.1371/journal.pone.0036207>.
- Pereira, J.M., Almeida, P.S.de, Sousa, A.V.de, Paula, A.M.de, Machado, R.B., Gurgel-Gonçalves, R., 2013. Climatic factors influencing triatomine occurrence in Central-West Brazil. *Mem. Inst. Oswaldo Cruz* 108, 335–341. <https://doi.org/10.1590/S0074-02762013000300012>.
- R Core Team. (2021). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Reeves, W.K., Miller, M.M., 2020. A new state record for *Triatoma sanguisuga* (Leconte) (Hemiptera: reduviidae) from Wyoming, U.S.A. *Comp. Parasitol.* 87 (1), 118–120. <https://doi.org/10.1654/1525-2647-87.1.118>.
- Schmidt, J.O., Miller, M.L., Klotz, S.A., 2022. Seasonal flight pattern of the kissing bugs *Triatoma rubida* and *T. protracta* (Hemiptera: reduviidae: triatominae) in Southern Arizona, United States. *Insects* 13 (3), 265. <https://doi.org/10.3390/insects13030265>.
- Sjogren, R.D., Ryckman, R.E., 1966. Epizootiology of *Trypanosoma cruzi* in southwestern North America. 8. Nocturnal flights of *Triatoma protracta* (Uhler) as indicated by collections at black light traps (Hemiptera: reduviidae: triatominae). *J. Med. Entomol.* 3 (1), 81–92. <https://doi.org/10.1093/jmedent/3.1.81>.
- Sotthibandhu, S., Baker, R.R., 1979. Celestial orientation by the large yellow underwing moth, *Noctua pronuba* L. *Anim. Behav.* 27, 786–800. [https://doi.org/10.1016/0003-3472\(79\)90015-0](https://doi.org/10.1016/0003-3472(79)90015-0).
- Stokes, M.K., Slade, N.A., Blair, S.M., 2001. Influences of weather and moonlight on activity patterns of small mammals: a biogeographical perspective. *Can. J. Zool.* 79 (6), 966–972. <https://doi.org/10.1139/z01-059>.
- TexasET Network. (2020). <https://texaset.tamu.edu/>.
- The Meteorological Resource Center. (2020). [http://www.webmet.com/met\\_monitoring/622.html](http://www.webmet.com/met_monitoring/622.html).
- The Weather Channel. (2020). The weather channel. <https://weather.com/forecast/national>.
- Time and Date. (2020). <https://www.timeanddate.com/astronomy/moon/light.html>.
- Updyke, E.A., Allan, B.F., 2018. An Experimental evaluation of cross-vane panel traps for the collection of sylvatic triatomines (Hemiptera: reduviidae). *J. Med. Entomol.* 55 (2), 485–489. <https://doi.org/10.1093/jme/tjx224>.
- Vazquez-Prokopec, G.M., Ceballos, L.A., Kitron, U., Gürtler, R.E., 2004. Active dispersal of natural populations of *Triatoma infestans* (Hemiptera: reduviidae) in rural northwestern Argentina. *J. Med. Entomol.* 41 (4), 614–621. <https://doi.org/10.1603/0022-2585-41.4.614>.
- Vazquez-Prokopec, G.M., Ceballos, L.A., Marcet, P.L., Cecere, M.C., Cardinal, M.V., Kitron, U., Gürtler, R.E., 2006. Seasonal variations in active dispersal of natural populations of *Triatoma infestans* in rural north-western Argentina. *Med. Vet. Entomol.* 20 (3), 273–279. <https://doi.org/10.1111/j.1365-2915.2006.00637.x>.
- Verheijen, F.J., 1960. The mechanisms of the trapping effect of artificial light sources upon animals. *Arch. Néerl. Zool.* 13 (1), 1–107. <https://doi.org/10.1163/036551660X00017>.
- Walecx, E., Suarez, J., Richards, B., Dorn, P.L., 2014. *Triatoma sanguisuga* blood meals and potential for Chagas disease, Louisiana, USA. *Emerg. Infect. Dis.* 20 (12), 2141–2143. <https://doi.org/10.3201/eid2012.131576>.
- Williams, C.B., 1936. The influence of moonlight on the activity of certain nocturnal insects, particularly of the family Noctuidae, as indicated by a light trap. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 226 (537), 357–389. <https://doi.org/10.1098/rstb.1936.0010>.
- Wozniak, E.J., Lawrence, G., Gorchakov, R., Alamgir, H., Dotson, E., Sissel, B., Sarkar, S., Murray, K.O., 2015. The biology of the triatomine bugs native to South Central Texas and assessment of the risk they pose for autochthonous Chagas disease exposure. *J. Parasitol.* 101 (5), 520–528. <https://doi.org/10.1645/15-748>.
- Yela, J.L., Holyoak, M., 1997. Effects of moonlight and meteorological factors on light and bait trap catches of noctuid oths (Lepidoptera: noctuidae). *Environ. Entomol.* 26 (6), 1283–1290. <https://doi.org/10.1093/ee/26.6.1283dormlent>.