

Association of Anthropogenic Land Use Change and Increased Abundance of the Chagas Disease Vector *Rhodnius pallescens* in a Rural Landscape of Panama

Nicole L. Gottdenker,* José E. Calzada, Azäel Saldaña, and C. Ronald Carroll

Department of Pathology, College of Veterinary Medicine, and Odum School of Ecology, The University of Georgia, Athens, Georgia;
Department of Parasitology, Instituto Conmemorativo Gorgas de Estudios de la Salud, Panama City, Panama

Abstract. Anthropogenic disturbance is associated with increased vector-borne infectious disease transmission in wildlife, domestic animals, and humans. The objective of this study was to evaluate how disturbance of a tropical forest landscape impacts abundance of the triatomine bug *Rhodnius pallescens*, a vector of Chagas disease, in the region of the Panama Canal in Panama. *Rhodnius pallescens* was collected (n = 1,186) from its primary habitat, the palm *Attalea butyracea*, in five habitat types reflecting a gradient of anthropogenic disturbance. There was a high proportion of palms infested with *R. pallescens* across all habitat types (range = 77.1–91.4%). Results show that disturbed habitats are associated with increased vector abundance compared with relatively undisturbed habitats. Bugs collected in disturbed sites, although in higher abundance, tended to be in poor body condition compared with bugs captured in protected forest sites. Abundance data suggests that forest remnants may be sources for *R. pallescens* populations within highly disturbed areas of the landscape.

INTRODUCTION

Anthropogenic land use change influences the distribution, abundance, and behavior of disease vectors.^{1,2} There is a growing body of evidence that habitat disturbance resulting from anthropogenic land use change can lead to an increase in vector abundance, and in many cases, increased risk of disease transmission.^{3–6} In the northeastern Peruvian Amazon, the malaria vector *Anopheles darlingi* human biting rate in deforested areas near recent road development was much greater than in forested areas.⁷ Forest loss and agricultural development in the Peruvian Amazon have also been associated with increased mosquito abundance caused by an increase in standing water held by plants (e.g., bromeliads and pineapple).⁸ Many species of anopheline mosquito malaria vectors can increase in abundance in response to increased sunlight availability, a common occurrence in deforested areas. In deforested African highland agricultural sites, increased malarial vector survival rate and juvenile survival rate were observed.⁹ Habitat fragmentation, defined as breaking apart of habitat, independent of habitat loss, is a manifestation of landscape disturbance.¹⁰ Forest fragmentation has been associated with increased tick vector abundance and prevalence of the Lyme disease agent *Borellia burgdorferi* in tick vectors.^{11,12} Anthropogenic land use changes in Israel have been associated with increased abundance of the cutaneous leishmaniasis vector *Phlebotomus papatasi* and increased infection prevalence of *Leishmania major* in rodent hosts.¹³

In this study, we examine relationships between anthropogenic habitat disturbance and population characteristics of the triatomine bug *Rhodnius pallescens* in a rural landscape of Panama. For the purposes of this study, a landscape is defined as a spatially explicit area comprised of interacting structurally and spatially heterogeneous components or ecosystems that may vary in arrangement and architecture.¹⁴ We define habitats as qualitatively distinct vegetation types comprising the landscape.

Rhodnius pallescens is considered to be the primary vector for *Trypanosoma cruzi* infections of humans and animals in Panama, some areas of Costa Rica, and Colombia.^{15–19} *Trypanosoma cruzi*, the agent of Chagas disease, is a major cause of heart disease and general morbidity among humans in Latin America, with estimates of 8–15 million infected persons.^{20,21} Many studies have observed a close association between *Rhodnius* species, palms, and Chagas disease risk.^{22–26} The palm *Attalea butyracea* provides the primary breeding habitat of *R. pallescens*.²⁷ *Attalea butyracea* is ubiquitous throughout lowland tropical forest landscapes in Panama, ranging from intact forests to deforested areas. High densities of *A. butyracea* within forests are also commonly associated with anthropogenic activities, such as hunting of seed predators of these palms and past agricultural activity.²⁸

The intimate *R. pallescens*–palm relationship and wide distribution throughout the landscape is ideal to evaluate how land use may affect vector abundance across a gradient of land use disturbance. Human settlement and agricultural production throughout the 20th century has transformed the once highly forested rural landscape outside of protected forests in the Panama Canal Watershed into a land mosaic dominated by cattle pasture, lesser amounts of cropland, human settlement, and forest remnants (Figure 1).^{29,30} This recent forest landscape disturbance may increase human contact with vector-borne parasites such as the Chagas disease agent *T. cruzi* by increasing vector invasion and re-invasion into domiciles from sylvatic foci, *A. butyracea* palms.³¹ An extensive meta-analysis of *Rhodnius* species suggests that forest habitat loss may increase contact between *Rhodnius* and humans.³² Specifically, we investigated how *R. pallescens* relative abundance and body condition change in relation to habitat types reflecting a gradient of anthropogenic land disturbance in the area of the Panama Canal.

METHODS

Study area, habitat types, and study sites. The study area comprised the landscape surrounding the Panama Canal, consisting of habitat components of protected late secondary moist tropical forest adjacent to the canal flanked by a mosaic of disturbed habitat types whose potential vegetation

*Address correspondence to Nicole L. Gottdenker, Department of Pathology, School of Veterinary Medicine, The University of Georgia, 501 DW Brooks Drive, Athens, GA 30602. E-mail: gottdenk@gmail.com

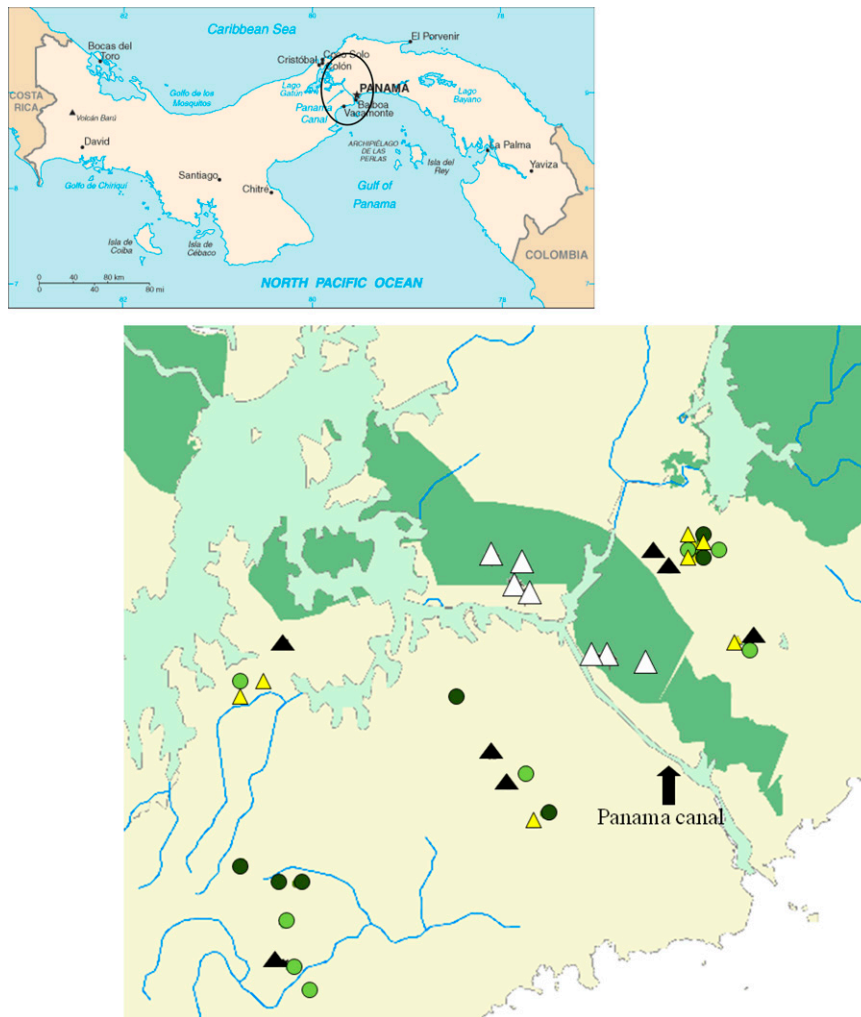


FIGURE 1. Panama Canal Area and approximate location of study sites/habitat types. White triangle = late secondary contiguous forest; dark circle = mid secondary forest remnant; light circle = early secondary forest patch; yellow triangle = pasture; black triangle = peridomiliary area. This figure appears in color at www.ajtmh.org.

is lowland moist tropical forest.³³ These highly disturbed areas consist of patches of forest remnants primarily located in riparian areas, habitat patches in early phases of forest regeneration (abandoned pasture), cattle pasture, and human settlements (domiciles) (Figure 1). Five habitat types were sampled for *R. pallescens*: contiguous late secondary forest (low disturbance), anthropogenically disturbed patches of early secondary forest patches, mid-secondary forest remnants, cattle pasture, and peridomiliary areas. Contiguous late secondary forest sites were located in a protected national park adjacent to the Panama Canal. These sites have a known land use history and forest age (approximately 75–100 years old).³⁰ Early secondary forest fragments were areas of abandoned pasture or cropland undergoing forest succession. These sites were approximately 5–30 years old, and most trees within the early secondary sites did not exceed 10 meters in height. There was also a predominance of lianas in most of these early secondary forest fragments. Mid-secondary forest remnants or fragments were forest patches remaining after large-scale deforestation of late secondary or mature forest. Most of these mid-secondary patches were highly disturbed, as most of the economically valuable adult trees were previously

harvested from these sites, and the floor of most of these forest patches were heavily trampled by cattle. Peridomiliary areas consisted of home gardens or yards located within 100 meters of a human dwelling. The gardens and yards surrounding domiciles were highly variable, some with well-manicured lawns and others with tall grass or located near a forest patch. Seven comparable sites chosen from each of the five habitat types, comprising total of 35 sites, were sampled for *R. pallescens* in different habitats along the western and eastern border of the Panama Canal Area (Figure 1). Individual sites were at least 200 meters apart from each other, based on an estimated maximum flight distance for *Rhodnius* sp., with most sites located greater than 1 km apart from each other.³⁴ Replicate sites from comparable habitat types were located at least 600 meters apart from one another. Study sites were spread over an area of approximately 600 km². Palms were sampled once from each site during the wet season, during May–December 2007, to control for possible effects of season on *R. pallescens* abundance. Sites from multiple habitat types were sampled within each month, and an attempt was made to spread the sampling of different habitat types evenly across the wet season. The sites chosen were areas where the palm

Attalea butyracea was present. Across this landscape, palms are patchily distributed.

Palm sampling for *R. pallescens*. At each location, five palms were sampled for the relative density of *R. pallescens*; an adult *A. butyracea*, and the four nearest accessible adult *A. butyracea* palms. The initial palm was selected by choosing the nearest palm to a random direction and distance less than 20 meters from the observer. The height at the top of the crown base, number and ripeness of fruit racemes, and presence of animal (bird and/or mammal nests or resting sites) were also recorded for each palm.

Three baited traps, modified from a method described by Abad-Franch and others,²⁶ were placed within the crown of each palm, left for 24 hours, and checked for *R. pallescens* the next day.^{26,35,36} Palm crowns were accessed with a 20-foot ladder or by climbing the palm tree with a rope and harness tree-climbing technique modified for palms. The modification of traps included a food and a hydration source that were provided for mice within the traps, and traps were covered with a small sheet of plastic to provide protection from direct sun and rain. Sampling methods are shown in Figure 2.

After collecting the baited traps, the palm crowns were searched for 10 minutes for bugs by a skilled person. The number and stage (first through fifth stage nymphs, adult) of *R. pallescens* was recorded for each tree. We also recorded the sex of adult bugs, weight (mg), length (mm), and nutritional status of bugs (fourth and fifth stage nymphs and adults) by evaluating abdominal distension and the presence and location of a blood meal within the digestive tract. Bugs were assigned the following body condition scores based on evaluation of degree of abdominal distension and blood meal present in the gut: 1 = engorged; 2 = good, some abdominal distension blood in the foregut, midgut, and hindgut; 3 = moderate, no abdominal distension, moderate amount of blood in the midgut, hindgut, and rectal ampulla; 4 = thin, thin abdomen, starved or small amount of blood present in hindgut or rectal ampulla.

Evaluation of trapping efficiency. To evaluate the efficiency of our trapping method, we performed our described trapping method (mouse-baited traps with direct search) on eight palm trees separated from the sites that were included in the sampling scheme. The trees were chopped down, fully dissected, and carefully searched for *R. pallescens* that were

not caught in the traps. Specifically, we dissected the full base of the palm crown to actively search for bugs. The number of bugs captured by trap and search was then compared with total number of palms with palm dissection and traps by using a generalized linear model with quasi-poisson errors appropriate for count data.

Satellite imagery for estimation of normalized difference vegetation index. A normalized difference vegetation index (NDVI), aspect, and altitude were measured for each site by analysis of 2002 satellite image data of Panama in ArcGIS versions 9.2 and 9.3 (ESRI, Redlands, CA). A relatively cloud free image of the study area (the best image that could be found) was downloaded from 2002 Landsat 7 satellite imagery from the U.S. Geological Service, and reflectance data was collected from the image after geometric rectification and atmospheric correction. The NDVI was calculated from the acquired satellite image reflectance data by using Erdas Imagine 9.0 software (Leica Geosystems, Norcross, GA). Higher NDVI values often represent increase in density of leafy green vegetation, making them suitable measurement for forest cover and/or plant growth (http://earthobservatory.nasa.gov/Features/Measuring_Vegetation). The resolution used for calculating NDVI for each site was 90 meters. A Mantel test was used to investigate relationships between distance between sites and bug abundance.

Data analysis. Parametric and non-parametric statistical analyses were performed in R 2.7.1 (2004–2008, the R Foundation for Statistical Computing, <http://www.R-project.org>). Because of the hierarchical nature of the data (bug samples taken from five palms nested within a site, and site replicates nested within each habitat type), linear mixed effects models were used to analyze the proportion of palms infested by bugs and bug abundance. To analyze the relationship between habitat type and the proportion of palms infested by bugs, we used a generalized linear mixed model with a fixed effect (habitat type), a random effect (site), and binomial errors, fit by the Laplace approximation. The Laplace approximation is an appropriate generalized linear mixed model fitting technique for poisson or binomial data where there are less than three random effects and the minimum number of successes or failures is greater than five for binomial distributions.³⁷ To test the effect of habitat type on bug abundance, we used a Laird-Ware formulation of a generalized linear mixed model with a fixed effect (habitat type), two nested levels of random effects (individual palm nested within site), and Poisson errors.³⁸ Penalized quasi-likelihood was used to fit this model because it was considered appropriate for poisson data with a mean bug abundance per tree greater than five.³⁷ Habitat type was considered a fixed effect in the models because it was an overall invariant classification scheme.

RESULTS

Trap efficiency. The number of bugs captured using the trap-direct search method was positively associated with the total number of bugs within the palm (trap-direct search plus tree dissection) ($n = 8$ palms) (Figure 3). There was also a positive, yet non-significant correlation between the number of bugs caught by trap-direct search and the number of bugs caught during tree dissection (Spearman's rank correlation $\rho = 0.67$, $P = 0.07$). Both findings indicate that the trapping method used in this study (trap-direct search) was an adequate



FIGURE 2. Field methods used in the study, Panama. **Left**, Capture of *Rhodnius pallescens* in palms. **Right**, Adult and nymphs of *R. pallescens* captured with a baited sticky.

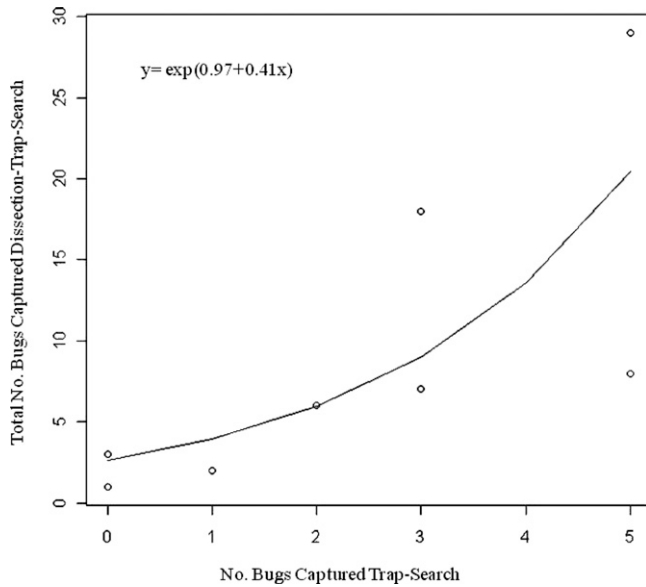


FIGURE 3. Trap-search method efficiency test (n = 8 palms dissected) and relationship between the number of bugs captured by the trap-search method combined with the total number of bugs captured with trap-search-tree dissection (best fit line from generalized linear model with quasi-poisson errors), Panama.

representation of relative within-palm bug abundance. On average, 28% (range = 0–43%) of the total number of bugs found were caught with the baited traps only.

Palm infestation with *R. pallescens*. Across all habitat types, we recovered *R. pallescens* from 80.0% (140 of 175) of palms. The percentage of palms infested with *R. pallescens* was high throughout anthropogenically disturbed habitats, ranging from 77.1% in peridomiciliary habitats to 91.4% in mid-secondary forest fragments; the lowest proportion (57.1%) of infested palms was in contiguous forests (Table 1). There was a significant and moderate dependence between habitat type and the number of palms in which *R. pallescens* was present (Pearson’s $\chi^2 = 16.786$, degrees of freedom [df] = 4, $P = 0.002$). The estimated proportion of infested palms was significantly greater in mid-secondary forest remnants (generalized linear mixed effects model, binomial errors, $P = 0.02$), and marginally

significant in early secondary forest fragments and cattle pasture than in contiguous forests (Table 2). The proportion of palms infested with *R. pallescens* in mid-secondary and early secondary fragmented forests combined (n = 70 palms examined) was significantly greater than the number of palms infested with *R. pallescens* in contiguous forests (n = 35 palms examined) ($\chi^2 = 11.698$, df = 1, $P = 0.00062$, by sample test for equality of proportions with continuity corrections).

Relative abundance and distribution of *R. pallescens*. The mean number of bugs captured per site differed significantly between habitat types (Kruskal-Wallis $\chi^2 = 28.1$, df = 4, $P < 0.0001$). A generalized linear mixed effects model (Table 3 and Figure 4) applied to the data (poisson errors) for the relationship between bug abundance and habitat type demonstrates significant differences between the number of bugs captured in contiguous forests as compared with early secondary forest fragments (fixed effects, $P = 0.004$), mid-secondary forest fragments (fixed effects, $P < 0.003$), and cattle pasture (fixed effects, $P = 0.01$). There was a slight negative, yet significant ($P = 0.02$) relationship between NDVI and estimated bug abundance by the generalized linear mixed effects model (Table 4). There was no significant spatial autocorrelation in bug abundance between collection sites (n = 35 sites; $P = 0.21$, by Mantel test).

Nymph:adult ratio. In all habitat types, the frequency of nymphs was greater than that of adults (Pearson’s $\chi^2 = 10.4291$, df = 4, $P = 0.03$). However, there was no apparent significant difference between the nymph:adult ratio and habitat type (fixed effects, minimum $P = 0.30$). The colonization index (number of palms with nymphs/number of palms with *R. pallescens*) was high throughout all habitat types and ranged from 0.85 in contiguous forests to 1.00 in cattle pastures (Table 1).

Sex ratio of adult bugs. Overall, there was no significant difference in the relative number of male and female bugs captured across all habitat types (n = 181; $\chi^2 = 0.280$, df = 1, $P = 0.60$). There was no evidence of dependence between *R. pallescens* sex ratio and habitat type (n = 181; $\chi^2 = 5.27$, df = 4, $P = 0.26$).

Body condition. There was a dependent relationship between habitat type and the frequency of bugs in each qualitative body condition class (engorged, good, moderate, thin/starved) ($P < 0.0001$, by Fisher’s exact test). The proportion of bugs

TABLE 1

Rhodnius pallescens palm infestation rates, abundance, density, and population characteristics, Panama*

| Variable | Contiguous | Peridomicile | Early secondary | Mid-secondary | Pasture | Total |
|---|-----------------|------------------|------------------|------------------|------------------|------------------|
| % Palms infested with <i>Rhodnius</i> † | 57.1 (20/35) | 77.1 (27/35) | 85.7 (30/35) | 91.4 (32/35) | 88.6 (31/35) | 80 (140/175) |
| No. bugs captured | 73 | 201 | 299 | 346 | 267 | 1,186 |
| Mean no. bugs captured/site (95% CI)‡ | 10.4 (8.2–13.1) | 28.7 (24.9–33.0) | 42.7 (38.0–47.9) | 49.4 (44.3–55.0) | 38.1 (37.7–43.0) | 33.8 (32.0–35.9) |
| Overall density of bugs per habitat type§ | 2.06 | 5.74 | 8.54 | 9.86 | 7.63 | 6.78 |
| Mean density of bugs per infested palm¶ (95% CI) | 3.65 (2.9–4.6) | 7.44 (6.5–8.6) | 9.97 (8.9–11.2) | 10.81 (9.7–12.0) | 8.61 (7.6–9.7) | 8.47 (8.0–9.0) |
| No. of bugs/trap night (no. trap nights) | 0.56 (104)# | 1.91 (105) | 2.85 (105) | 3.29 (105) | 2.53 (105) | 2.3 (524) |
| No. adults captured | 12 | 48 | 65 | 68 | 35 | 228 |
| No. nymphs captured | 46 | 153 | 234 | 277 | 232 | 942 |
| Total nymph:adult ratio | 3.83 | 3.19 | 3.62 | 4.07 | 6.63 | 4.12 |
| Colonization index** | 0.85 | 0.93 | 0.90 | 0.94 | 1.00 | 0.93 |
| Mean ± SD weight/length ratio (mg/mm) of N4, N5, and adults | 5.10 ± 2.32 | 2.77 ± 0.42 | 3.91 ± 2.24 | 3.64 ± 2.45 | 4.08 ± 1.56 | 3.97 ± 2.2 |

* CI = confidence interval.
 † No. palms with bugs/total no. palms examined.
 ‡ Seven sites per habitat type.
 § No. bugs captured/no. palms, sampled per site.
 ¶ Mean no. of bugs captured per infested palm.
 # One trap predated.
 ** No. palms with nymphs/no. palms with triatomines.

TABLE 2

Results of a generalized linear mixed model evaluating the relationship between the proportion of palms in which *Rhodnius pallescens* was detected and habitat type, Panama*

| Effects | Estimate | Standard error | z-value | P |
|--------------------------|----------|----------------|---------|--------|
| Fixed effects | | | | |
| Intercept | 0.4516 | 0.7869 | 0.5739 | 0.5660 |
| Early secondary fragment | 2.3969 | 1.2691 | 1.8886 | 0.0589 |
| Mid secondary remnant | 3.3053 | 1.4721 | 2.2452 | 0.0248 |
| Cattle pasture | 2.4555 | 1.2535 | 1.9589 | 0.0501 |
| Peridomicile | 1.5799 | 1.1888 | 1.3291 | 0.1838 |

*Fixed effect = habitat; random effect = site; family = binomial; link = logit, fit by the Laplace approximation.

that were in good condition and engorged was significantly greater in contiguous forest habitats ($n = 37, 59.5\%$) compared with disturbed habitats ($n = 278, 6.8\%$) (two-sample test for equality of proportions with continuity correction, $\chi^2 = 95.2, P < 0.0001$) (Figure 5). The mean ranks of the weight:length ratio of adult and nymph (fourth to fifth stage nymphs) *R. pallescens* captured in continuous forests was higher than bugs captured in anthropogenically disturbed habitat types ($W = 7408, P < 0.001$, by Wilcoxon rank-sum test). There was no significant difference between the mean \pm SD ranks of weight:length ratio measurements between males ($4.78 \pm 1.54, n = 87$) and females ($4.9 \pm 1.54, n = 94$) ($W = 4186, P = 0.78$, by Wilcoxon rank-sum test).

DISCUSSION

It is well established that *A. butyracea* palms are the primary ecotype for *R. pallescens* throughout their range in Central America and northern South America.^{15,32} Palm trees are considered to be a risk factor for Chagas disease in neotropical landscapes.^{32,39–42} However, less is understood regarding how vector abundance in palms varies relative to land use/anthropogenic disturbance surrounding their microhabitats. We present evidence that anthropogenic activity, resulting in the creation of forest remnants, regenerating forests, cattle pasture, and domiciliary areas, is associated with increased presence and abundance of *R. pallescens* in *A. butyracea* palms.

The percentage of palms infested with *R. pallescens* within and among each habitat type was relatively high (range = 57.1–91.4%), compared with other studies of triatomines palm infestations.^{41,43} In Ecuador, *R. ecuadoriensis* infestation of *Phytelephas aequatorialis* tagua palms was 23% of 110 palms examined. Similar to our study, there was a higher percentage of *R. ecuadoriensis* palm infestation of tagua palms *Phytelephas aequatorialis* from deforested sites in Ecuador.²⁶ Unlike the present study, where there was a high palm infestation with

TABLE 3

Results of a generalized linear mixed model evaluating the relationship between the number of *Rhodnius pallescens* captured and habitat type, Panama*

| Effects | Estimate | Standard error | t-value | P |
|--------------------------|----------|----------------|---------|--------|
| Fixed effects | | | | |
| Intercept | 0.9509 | 0.2933 | 3.2422 | 0.0015 |
| Early secondary fragment | 1.1324 | 0.3665 | 3.0892 | 0.0043 |
| Mid-secondary remnant | 1.1683 | 0.3666 | 3.1872 | 0.0033 |
| Cattle pasture | 1.0016 | 0.3687 | 2.7163 | 0.0108 |
| Peridomicile | 0.6543 | 0.3843 | 1.7024 | 0.0990 |

*Fixed effect = habitat; random effects = individual palms nested within sites; family = poisson(loglink) fit using maximum likelihood.

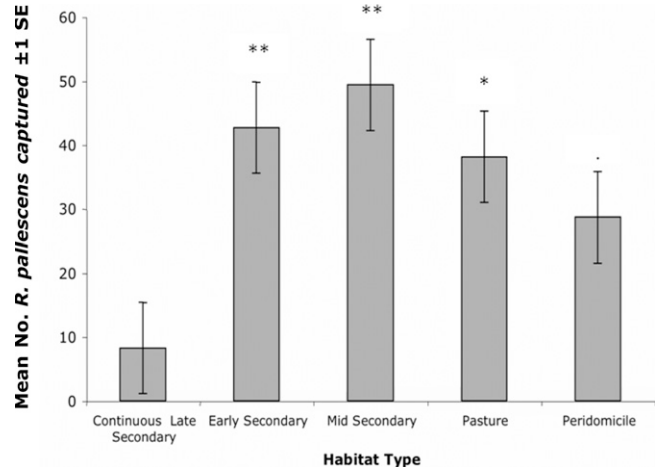


FIGURE 4. Mean number of *Rhodnius pallescens* captured per site across different habitat types ($n = 7$ sites per habitat type) in the Panama Canal Area (generalized linear mixed model significance codes: ** = < 0.005 , * = < 0.05 , • = < 0.1).

R. pallescens in forest fragments, there was no evidence of infestation of tagua palms by *R. ecuadoriensis* in forest remnants in Ecuador.²⁶ *Rhodnius neglectus* infestation rates in *Mauritia* palms in Brazil ranged from 18.6% to 37%.⁴³ In a previous study of *R. pallescens* infestation of *A. butyracea* palms ($n = 30$) examined from an urban and rural area of Panama, the proportion of infested palms from urban, rural, and forest areas were 100%, 80%, and 90%, respectively.⁴⁴ Similar to the present study, high palm infestation rates with *Triatoma sordida* (96.2%) were observed in northeastern Argentina.⁴² It is possible that *Rhodnius* sp. palm infestation rates in our study, although high, may be underestimated. In the Amazon, occupancy modeling of *Rhodnius* in palms concluded that the observed proportion of infested palms were much lower than estimates of palm infestation when imperfect vector detection was included in the analysis.⁴¹

A regional and landscape-level study of *Rhodnius* spp. in palm trees across the Amazon basin demonstrate a higher estimated occupancy of *Rhodnius* spp. in palms in rural versus urban areas.⁴¹ Unlike our findings, that study did not find a significant difference in *Rhodnius* spp. palm occupancy rates in rural areas versus forest settings. However, forests sampled in the Amazonian study were actually forest fragments, not contiguous forests.⁴¹ Factors associated with increased triatomine abundance and infestation in palm trees include a large amount of decaying organic matter and vegetative growth at the base of the palm crown and presence of animal nests in the palm such as bird nests.^{16,26,41,42,44,45} Interestingly, *Rhodnius* spp. occupancy and abundance within palms were higher in an area of Amazonia with relatively fertile soils than less fertile areas,

TABLE 4

Results of a generalized linear mixed model examining the relationship between normalized difference vegetation index and the total number of *Rhodnius pallescens* captured per site (175 palms sampled across 35 sites), Panama*

| Effects | Estimate | Standard error | z-value | P |
|-------------------------|----------|----------------|---------|----------------------|
| Fixed effects intercept | 2.437 | 0.5629 | 4.33 | 1.5×10^{-5} |
| NDVI | 0.0078 | 0.0034 | -2.28 | 0.022 |

*NDVI = normalized difference vegetation index.

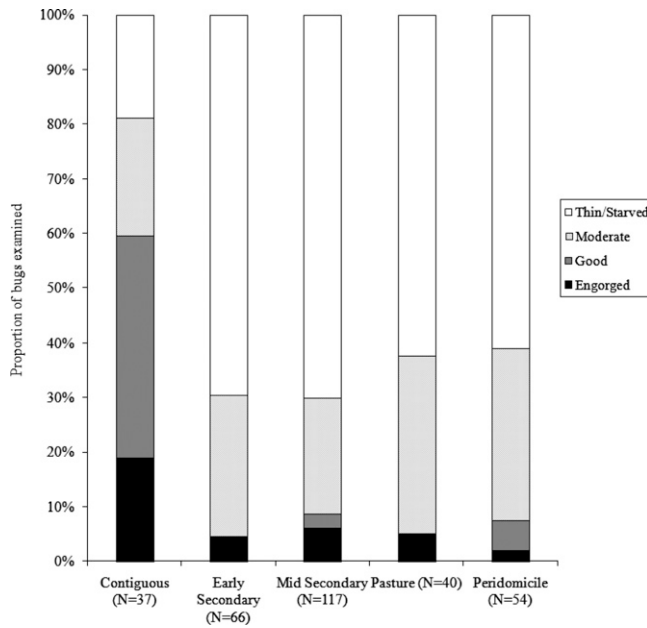


FIGURE 5. Qualitative body condition indices of *Rhodnius pallescens* captured in different habitat types, Panama.

suggesting that edaphic factors may also influence triatomine abundance in palms.⁴¹

In the present study, habitat type and a related measure of forest/vegetation cover, the NDVI, correlated with *R. pallescens* abundance in palm trees because there was a significantly greater number of bugs captured in anthropogenically dominated habitats compared with contiguous late secondary forests. Additionally, there was a negative relationship between NDVI and vector abundance (Table 4); the highest NDVI values were found for contiguous forest sites. Similarly, in studies of *R. neglectus* in the palm *Mauritia flexuosa*, there was increased bug abundance in palm trees in rural areas versus sylvatic environments.⁴⁶ In fragmented and deforested landscapes, the highest *R. pallescens* abundance was in mid-secondary and early-secondary forest fragments, with lower bug abundances in cattle pasture and peridomiciliary areas. The lower mean abundance in peridomiciliary sites may be caused by a greater range of total bug abundance per site caused by the diverse nature of the peridomiciliary sites. There was also variation in the way that each domiciliary site was maintained (well-manicured lawns, adjacent to cattle pasture, and some sites near forest patches) and in the quality of houses and presence of domestic animals (from a few dogs and chickens to a large number of domestic fowl and dogs) surrounding homes in peridomiciliary areas.

Our data indicate that mid-secondary forest remnants and early secondary forest patches support a relatively high abundance of *R. pallescens*. Mid-secondary forest remnants are scattered throughout the pastoral landscapes in the Panama Canal Area. These forest remnants are primarily riparian and surrounded by a matrix of cattle pasture, agriculture, rural dwellings, or dwellings at the suburban/rural interface. Early secondary forests originate from regenerating pasture, but may have some large woody tree species and high densities of palms. Forest patches in primarily deforested rural areas may provide hiding places from potential predators, water resources, and protection from temperature extremes.

Additionally, fruiting trees such as palms within these forest patches may provide important nutritional sources for many vertebrate species. Forest remnants may serve as key resources for insectivorous birds and mammals.⁴⁷ Forest species that can live in edge habitats can invade fragments or remnants, thus increasing local population densities of animals.⁴⁸

Forest patches in deforested landscapes often support relatively high mammal densities caused by alterations of trophic structure by mesopredator release (an increased in medium-sized generalist omnivores in the deforested matrix and forest fragments in part caused by loss of top predators) and supplemental resources (crops, human food waste) provided by human activities within the fragmented landscape.⁴⁹ Some animals that respond positively to forest fragmentation may not be commonly hunted for food, and can maintain populations in deforested landscapes. Forest patches may also be used as an additional refuge for animals that may be dispersing or moving in an agricultural matrix, and for permanent residents of these fragments.⁵⁰ Palm trees within forest patches may also provide key hiding and nesting sites for arboreal mammals and other animals, increasing vertebrate palm occupancy and providing a relatively stable and abundant food resource for *R. pallescens*, leading to the relatively high abundance of *R. pallescens* in early secondary forest sites and mid-secondary forest remnants.

Environmental effects, such as altered microclimate, may also lead to higher numbers of *R. pallescens* inhabiting forest remnants and pasture. In tropical forest fragments, edge effects such as lowered humidity can extend 100 meters into the fragment,⁵⁰ which can influence the abundance of *R. pallescens* that may benefit from the lower humidity versus excess humidity. High humidity is associated with increased mortality of *R. prolixus* caused by the fungal pathogen *Beauveria bassiana*.^{51,52} Relatively high humidity in contiguous forest environments may increase mortality and lower vector abundance.

Additionally, food web structure disruption (potential loss of natural enemies, predators and pathogens of *R. pallescens*) may support higher vector abundance in deforested landscapes. It is also possible that in there is a loss of ecological trophic complexity in deforested landscapes that leads to a loss of an intact suite of predators, pathogens, and specialized parasitoids from the ecosystem.⁴⁰ Understanding how parasitoids and pathogens of *R. pallescens* respond to ecological disturbance is an unexplored but important avenue for future investigation.

Compared with other habitat types, the nymph:adult ratio is lowest in cattle pastures. This observation could be caused by emigration of adults from pastures because there are less hosts to feed from in space and time, with adults emigrating from pastures at a high rate to areas with a more constant or reliable food supply or lowered adult survivorship in pastures. In cattle pasture, the colonization index is the highest of all habitat types, implying that many adult bugs may reproduce in pastures, yet do not reside for an extended period of time within them, possibly caused by higher mortality of adults in cattle pasture (sink habitat), or emigration to higher quality sites (forest fragments, peridomicile). Cattle pastures may thus act as population sinks for *R. pallescens* at a landscape scale. Alternatively, bugs may use palms in cattle pasture as stopover sites during migration to more suitable habitat patches.

Although it was not statistically significant, *R. pallescens* in contiguous forests tended to be in better physical condition

compared with bugs in fragmented landscapes. Because starved triatomine adults can have a higher dispersal probability or potential than fed bugs,⁵³ dispersal rates may be higher in fragmented landscapes, leading to a higher probability that bugs may enter human dwellings in search of a blood meal.

Study results suggest that anthropogenic land use change leads to a higher abundance of *R. pallescens* and that forest remnants may be sources for *R. pallescens* at a landscape scale in rural areas dominated by anthropogenic activity. Deforestation is hypothesized to increase contact between Chagas disease vectors and humans.^{32,39} It is important to emphasize that a higher abundance of *R. pallescens* in a habitat does not necessarily translate to increased human Chagas disease risk because socioeconomic and human behavioral factors are important to consider when evaluating disease risk to humans, as emphasized by studies of leishmaniasis in Costa Rica⁵⁴ and Lyme disease incidence in relation to forest fragmentation in Connecticut.¹²

It is unknown if these habitat-related effects on bug abundance vary seasonally. Season, climate, and relative humidity can influence triatomine dispersal.⁵⁵ However, samples were only collected during the wet season. It is possible that *R. pallescens* populations decrease during the dry season in deforested habitats because of excess sunlight, temperature extremes, and low humidity. In our study, differences in microhabitats (temperature and humidity) within the palm crown were not measured. Our study also did not capture long-term trends in bug abundance, body condition, and age structure that may be caused by climate-related (e.g., El Niño effects) fluctuations in host population abundance.

There is a need for further long term surveillance of *R. pallescens* populations in deforested and forested areas in Panama. Understanding how long-term variation in climate and rainfall interacts with habitat associated abundance is important in predicting and identifying further localized hotspots of bug abundance and potential *T. cruzi* transmission. Because of seasonal variations, global warming trends, and continued forest destruction, long-term monitoring of different habitat types at a landscape scale for triatomine vectors is needed throughout their range. This type of long-term integrated monitoring and control strategy has been used for *Triatoma infestans* populations in some rural areas of the Argentinean Chaco and has proven to be effective in reduction of Chagas disease vectors and risk to local inhabitants.⁵⁶

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Authors' addresses: Nicole L. Gottdenker, Department of Pathology, School of Veterinary Medicine, The University of Georgia, Athens, GA, E-mail: gottdenk@gmail.com. José E. Calzada and Azáel Saldaña, Department of Parasitology, Instituto Conmemorativo Gorgas de Estudios de la Salud, Apartado Postal 0816-02593, Panama City, Panama, E-mails: jcalzada@gorgas.gob.pa and asaldana@gorgas.gob.pa. C. Ronald Carroll, Odum School of Ecology, Ecology Building, The University of Georgia, Athens, GA, E-mail: ronecology@gmail.com.

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