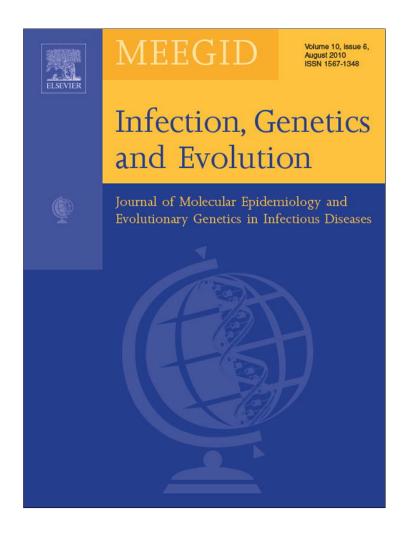
Provided for non-commercial research and education use. Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Infection, Genetics and Evolution 10 (2010) 720-726

Contents lists available at ScienceDirect



Infection, Genetics and Evolution

journal homepage: www.elsevier.com/locate/meegid



Analysis of the geographical distribution of *Triatoma vitticeps* (Stål, 1859) based on data of species occurrence in Minas Gerais, Brazil

Rita de Cássia Moreira de Souza^{a,*}, Liléia Diotaiuti^a, Marcelo Gustavo Lorenzo^a, David E. Gorla^b

^a Centro de Pesquisas René Rachou, Avenida Augusto de Lima, 1715, Belo Horizonte, Minas Gerais, 30190-002, Brazil ^b Centro Regional de Investigaciones Científicas y Transferencia Tecnológica (CRILAR), Entre Rios y Mendonza s/n, 5301 Anillaco, La Rioja, Argentina

ARTICLE INFO

Article history: Received 29 December 2009 Received in revised form 30 April 2010 Accepted 7 May 2010 Available online 21 May 2010

Keywords: Triatoma vitticeps Epidemiology Geographic distribution Environmental variables GIS Relative humidity Chagas disease

ABSTRACT

The purpose of this study was to determine the potential for infestation of man-made environments by *Triatoma vitticeps*, correlating the epidemiological importance of this species with that of others present in the Brazilian state of Minas Gerais. In addition, climatic variables that could help explain the distribution of this species and clarify its population dynamics were sought. This was done by carrying out a historical survey of the presence of *T. vitticeps* in artificial ecotopes, using data from the Fundação Nacional de Saúde (FUNASA). Monthly records of bioclimatic variables averaged for the period 1950–2000 and pixel size of 1 km × 1 km provided a reference for spatial distribution analysis. Annual rainfall and rainfall of the most humid trimester are the best indicators of the species distribution. To confirm the importance of these variables, *T. vitticeps* eggs were exposed to different levels of relative humidity. Hatching was found to vary significantly, and low humidity showed a significant negative effect on egg hatching. Our results demonstrate a strong association between *T. vitticeps* and high environmental humidity, which apparently acts as a limiting factor on the distribution of this triatomine.

© 2010 Elsevier B.V. All rights reserved.

1. Introduction

Triatomine bugs (Hemiptera: Reduviidae) are the vectors of *Trypanosoma cruzi*, the etiological agent of Chagas disease. Currently 140 species are recognized, within Triatominae grouped into 15 genera and five tribes, of which 128 species, 14 genera and five tribes occur in the Americas (Schofield and Galvão, 2009). The epidemiologically most important species are those that invade and colonize houses, as adaptation to man-made ecotopes is intimately related to the availability of shelters and abundance of bloodmeal sources (Diotaiuti, 2007).

Triatoma vitticeps is found in the Brazilian states of Bahia, Espírito Santo, Minas Gerais and Rio de Janeiro (Lent and Wygodzinsky, 1979; Silveira et al., 1984). It occurs in the Atlantic Forest areas and is considered a species of secondary importance in the transmission of *T. cruzi* to man. Studies carried out on *T. vitticeps* populations in Espírito Santo and Rio de Janeiro have demonstrated its high capacity to invade houses, and always presenting high rates of infection by *T. cruzi* – like flagellates (Santos et al., 1969, 2006; Sessa

E-mail addresses: rita@cpqrr.fiocruz.br (R.d.C.M. de Souza), diotaiuti@cpqrr.fiocruz.br (L. Diotaiuti). and Carias, 1986; Dias et al., 1989; Lorosa et al., 2008). Recently, Souza et al. (2008) demonstrated through biosystematic studies that there is considerable gene flow among domestic and sylvatic populations of this vector. Because of this movement, the triatomines effectively constitute a single population that periodically invades human dwellings, although intradomiciliary colonization is inefficient. Technical reports of the Fundação Nacional de Saúde (FUNASA) of Minas Gerais from 1990 to 1999 frequently includes captures of this vector in intra- and peridomiciliary ecotopes. The reports do not mention the characteristics of these colonizations in relation to preferred ecotopes, climatic determinants and spatial distribution that could help explain the dynamics of intra- and peridomiciliary populations.

The influence of environmental factors on the distribution and abundance of different insects species is widely recognized, being climatic variables (principally temperature and humidity) amongst the most influential on their vital functions (Gorla et al., 1997). The geographical distribution of most disease vectors is limited by climatic conditions (WHO, 1990). Changes in mean temperature and precipitation would have an impact on the population size and distribution of vectors, allowing the occupation of new areas or even permitting populations to alter their initial distribution by migrating from one area to another.

Recording of biophysical variables by remote sensors on satellites has provided a new tool that allows the spatial distribution of a species to be analyzed, providing information that can be used in the

^{*} Corresponding author at: Avenida Augusto de Lima, 1715 Barro Preto, Belo Horizonte, Minas Gerais, CEP: 30190-002, Brazil. Tel.: +55 31 3349 7761; fax: +55 31 3295 3115.

^{1567-1348/\$ -} see front matter © 2010 Elsevier B.V. All rights reserved. doi:10.1016/j.meegid.2010.05.007

monitoring and control of vectors. By means of this technique and subsequent discriminant analysis, it was possible to identify correctly 90% of the localities where Triatoma infestans (Klug, 1834) is present or absent (Gorla, 2002). This analysis selected six variables of highest weight for the analysis: four associated with air temperature, one with infrared radiation and a third with the vegetation index. Recently Carbajal de La Fuente et al. (2008) proposed a predictive model for the geographical distributions of Triatoma wygodzinskyi Lent 1951 and Triatoma pseudomaculata Corrêa & Espínola 1964. The analysis was based on biophysical variables obtained from the remote sensors AVHRR (Advanced Very High Resolution Radiometer) and MODIS (Moderate-resolution Imaging Spectroradiometer) aboard polar orbiting satellites. The hypothesis raised by these authors was that the distribution of the two species is defined by different environmental characteristics, related to temperature and vapor pressure deficit for the T. wygodzinskyi model and to vegetation index and ground surface temperature for that of *T. pseudomaculata*.

The relative humidity of the air (RH) is an environmental factor that could affect different aspects during the life of an insect, as already been shown for some triatomines species. Roca and Lazzari (1994) investigated the hygropreferences of nymph and adult T. infestans in RH gradients, as well as the influence of humidity on egg hatching and during ecdysis. Both nymphs and adults remained in areas with RH close to 0%, not changing their behaviour according to the time of day or fasting period. The insects also preferred low humidity during the periods of ecdysis and oviposition. When submitted to different RH values, no differences were observed in hatching. Guarneri et al. (2002) also carried out a study of hygropreference for Triatoma brasiliensis, a species found in semi-arid habitats in Brazil. Both the eggs and development of the nymphs of this species were affected by the highest RH (99.9%). However, egg hatching was reduced by the lowest RH (9.3%). In Panstrongylus megistus Burmeister 1835, Pires (2003) found that low humidity drastically affected hatching, increasing the post-hatching mortality of the nymphs, as well as interfering with feeding capacity and early moulting in this species. However, when placed in an RH gradient, P. megistus nymphs preferred humidities values close to 0% when recently engorged and during ecdysis, moving to areas with higher humidity when the fasting time was increased.

Species of secondary and even tertiary importance for Chagas disease transmission are commonly found inside houses nowadays (Diotaiuti, 2007). According to Dias (2006), the recent elimination of *T. infestans* by the Brazilian Programa de Controle da Doença de Chagas (PCDCh) and successive man-made environmental transformations may have promoted this process. This scenario may represent a new threat, increasing the risk of *T. cruzi* transmission to man by other triatomines.

Thus, the objective of the present study is to analyze the association between the geographic distribution of *T. vitticeps* and a set of environmental variables, and the influence of relative humidity to the species fertility.

2. Materials and methods

2.1. Data collection on T. vitticeps

To determine the potential for colonization of man-made environments by the vector, data on domiciliary and peridomiciliary captures by the Control Program (PCDCh-FUNASA) in Minas Gerais were examined. This information referred to the years 1979, 1985, 1990 and 1995 in all municipalities within the eight sanitary districts: Caratinga, Diamantina, Januária, Montes Claros, Pirapora, Teófilo Otoni, Uberaba and Varginha. Information on triatomine captures was only recorded when a municipality was positive for *T*. vitticeps and also included data on the principal vector by the time (*T. infestans*), the most frequent autochthonous species (*Triatoma sordida* Stål 1859 and *P. megistus*) and other species, categorized as "others" (*Rhodnius neglectus* Lent 1954, *Triatoma melanocephala* Neiva & Pinto 1923, *Triatoma maculata* Erichson 1848, *T. pseudomaculata*, *Panstrongylus geniculatus* Latreille 1811 and *Panstrongylus diasi* Pinto & Lent 1946). Data on infection and capture of adults and nymphs of *T. vitticeps* inside houses and in the peridomicile were also analyzed.

2.2. Spatial analysis

Environmental data. In order to analyze the association between the geographic distribution of *T. vitticeps* and environmental variables, a bioclimatic database available on the Worldclim site version 1.4 (http://www.worldclim.org) described by Hijmans et al. (2005), was used. These authors built the environmental database using interpolation of data obtained from a great variety of information sources, corresponding to monthly records for the period 1950–2000 and spatial resolution of 1 km × 1 km.

Environmental variables referred to temperature (BIO1: mean annual temperature; BIO2: mean daily temperature variation; BIO3: isothermality – daily/annual temperature variation; BIO4: seasonal temperature; BIO5: maximum temperature of the hottest month; BIO6: minimum temperature of the coolest month; BIO7: annual temperature variation; BIO8: mean temperature of the most humid trimester; BIO9: mean temperature of the driest trimester; BIO10: mean temperature of the hottest trimester; BIO11: mean temperature of the coolest trimester), precipitation (BIO12: annual precipitation; BIO13: precipitation of the most humid month; BIO14: precipitation in the driest month; BIO15: coefficient of variation for seasonal precipitation; BIO16: precipitation of most humid trimester; BIO17: precipitation of driest trimester; BIO18: precipitation of the hottest trimester; BIO19: precipitation of the coolest trimester) and elevation. Values of the mentioned variables were extracted from the three districts where T. vitticeps was captured (301 pixels) and in compatible areas of absence (100 pixels) of this vector, chosen at random. The absence pixels were selected from areas within the Minas Gerais state where the vector control program had never found T. vitticeps specimens. The number of absence (100) and presence (301) pixels were selected as reasonable sample sizes of the absence and presence areas.

Entomological data. The area of presence was taken as the group of 107 municipalities reported positive for T. vitticeps capture, according to the Control Program data. The georeferenced database and environmental variables were incorporated into a map of Minas Gerais state and its municipalities, obtained from the Instituto Brasileiro de Geografia e Estatística (www.ibge.gov.br) (Fig. 1). Positive municipalities for T. vitticeps were located in three sanitary districts: Caratinga, Teófilo Otoni and Montes Claros/ Diamantina. The two latter regional districts were grouped together because the capture rate in both was very low (Table 1). To obtain the matrix of absence, localities where T. vitticeps was not recorded by the Control Program, some municipalities in western Minas Gerais were randomly selected. Using the environmental variable values for localities of presence and absence, we carried out a stepwise discriminant analysis to identify the set of variables that best described the sites where this species occurred or was absent, with a significance level α = 0.05. This analysis was processed using the Statistica program. The estimation of the misclassification rate was carried out using a cross-checked classification routine that iteratively built the discriminant equations leaving one data point out of the analysis for each iteration before calculating the classification matrix (PAD module developed by Dujardin, 2008).

Author's personal copy

R.C.M. de Souza et al. / Infection, Genetics and Evolution 10 (2010) 720-726

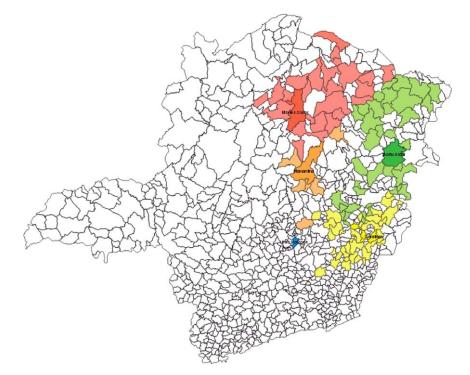


Fig. 1. Map of Minas Gerais showing municipalities where *T. vitticeps* was captured during routine surveys by PCDCh/FUNASA during 1979, 1985, 1990 and 1995. Municipalities of the sanitary districts of Montes Claros, Diamantina, Teófilo Otoni and Caratinga, are shown in red, orange, green and yellow, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

2.3. Effect of relative humidity on eggs hatching

An experiment was carried out to investigate whether relative humidity (RH) influences hatching of *T. vitticeps* eggs. Distilled water and saturated saline solutions were used to create different degrees of RH to which the eggs were exposed, i.e., distilled H₂O (100%), NaCl (70%), Ca(NO₃)₂ (52%), MgCl₂ (41%) and KOH (21%). The RH was measured using a thermohygrometer with a precision of $\pm 3\%$ (Testo 625, LenzKirch, Germany) at the end of the experiment. Eggs of *T. vitticeps* were collected from a laboratory colony maintained at CPqRR for at least 10 years and to which field captured specimens are regularly added. Eggs were gathered over three consecutive days and distributed randomly among five groups corresponding to the different humidity levels to be tested. Each group was placed in a small Petri dish, enclosed within another, larger Petri dish that contained the solutions mentioned above. A fine mesh net was placed over the small Petri dish to prevent nymphs from escaping into the solutions after hatching. The dishes were sealed to make them airtight and maintained in an

Table 1

Triatomines captured in the municipalities within the sanitary districts of Montes Claros, Caratinga, Teófilo Otoni and Diamantina, Minas Gerais, in 1979, 1985, 1990 and 1995 by the Chagas Disease Control Program of the Fundação Nacional de Saúde: number and percentages of triatomines corresponding to the total numbers captured during the period.

Districts	Species	1979 (%)	1985 (%)	1990 (%)	1995 (%)	Total (%)
Montes Claros	T. infestans		820 (9.3)	53 (0.5)	0	873 (3.4)
	T. sordida		6488 (73.6)	9571 (94.3)	6317 (98.4)	22,376 (88.2)
	T. vitticeps		376 (4.5)	203 (2.0)	11 (0.2)	590 (2.3)
	P. megistus		773 (8.8)	66 (0.6)	0	839 (3.3)
	Others		352 (3.9)	260 (2.6)	93 (1.4)	705 (2.8)
Caratinga	T. infestans	0	0	0	0	0
	T. sordida	0	0	0	0	0
	T. vitticeps	3 (3.0%)	297 (52.4)	270 (69.6)	183 (46.8)	753 (52.1)
	P. megistus	97 (97%)	268 (47.3)	115 (29.6)	208 (53.2)	688 (47.6)
	Others	0	2 (0.3)	3 (0.8)	0	5 (0.3)
Teófilo Otoni	T. infestans		3 (0.3)	0	0	3 (0.1)
	T. sordida		678 (55.8)	627 (61.1)	289 (67.5)	1594 (59.7)
	T. vitticeps		300 (24.7)	275 (26.8)	127 (29.7)	702 (26.3)
	P. megistus		145 (11.9)	58 (5.7)	5 (1.2)	208 (7.8)
	Others		95 (7.6)	63 (6.1)	7 (1.6)	165 (6.2)
Diamantina	T. infestans		0	0	0	0
	T. sordida		24 (22.9)	180 (30)	853 (95.9)	1057 (66.2)
	T. vitticeps		11 (10.5)	18 (3.0)	2 (0.2)	31 (1.9)
	P. megistus		69 (65.7)	394 (65.6)	18 (2.0)	481 (30.1)
	Others		1 (0.9)	9 (1.5)	17 (1.9)	27 (1.7)
Total						31,097

R.C.M. de Souza et al./Infection, Genetics and Evolution 10 (2010) 720-726

Table 2

Total number of triatomines captured, classified by species, in municipalities within the sanitary districts of Caratinga, Diamantina, Montes Claros and Teófilo Otoni in 1979, 1985, 1990 and 1995 by the Chagas' Disease Control Program of the Fundação Nacional de Saúde. Between brackets, percentage reduction or increase relative to number of triatomines captured in 1985.

	1979	1985	1990	1995	Total
P. megistus	97	1255	633 (-49.6%)	231 (-81.6%)	2216
T. infestans	_	823	53 (-93.6%)	0 (-100%)	876
T. sordida	_	7190	10,378 (+44.3%)	7459 (+3.7%)	25,027
T. vitticeps	3	984	766 (-22.2%)	323 (-67.2%)	2076
Others	_	450	335 (-25.6%)	117 (-74%)	902

incubator at 27 ± 2 °C with a controlled photoperiod (12:12 L/D). The incubator was illuminated by a 7 W fluorescent lamp during the light phase. The nymphs that hatched were maintained under the same conditions for 10 days, after which the hatching rate was determined. Two assays were conducted using 32 and 33 eggs, respectively, per RH tested (N = 325).

Data were analyzed using MINITAB software version 14.1, using a test of proportions with a significance level of P < 0.05.

3. Results

3.1. Collection of data on the occurrence of T. vitticeps in domestic and peridomestic environments

The number of triatomines captured by the Control Program in Minas Gerais during the study period is presented in Table 1. In 1979, T. vitticeps was only captured in Caratinga, so that none of the other species were counted in the remaining sanitary districts. The most abundant of the 31,097 triatomines captured was T. sordida (80.5%), with 88.2% of the insects belonging to this species collected in Montes Claros. P. megistus and T. vitticeps represented 7.1% and 6.7% of all triatomines captured, respectively. T. infestans, the most important species for the T. cruzi human transmission, was mainly collected in Montes Claros (3.4% of all triatomines), with small numbers captured in Teófilo Otoni (0.1%). According to the Control Program, these data probably represent post-control residual populations of previously larger infestations (data not reproduced here as triatomine capture results are only provided for sites at which T. vitticeps was found). Other species represented 2.9% of all triatomines captured. The occurrence of T. vitticeps is noteworthy in Caratinga and Teófilo Otoni, where it represented 52% and

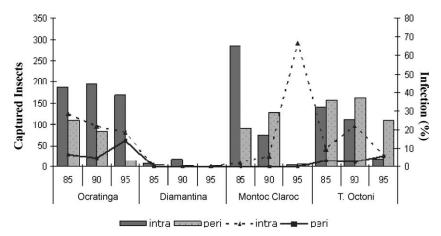


Fig. 2. Number of *T. vitticeps* captured (columns) and infection rate (lines), indoors and in the peridomicile, in four sanitary districts of the state of Minas Gerais in 1985, 1990 and 1995.

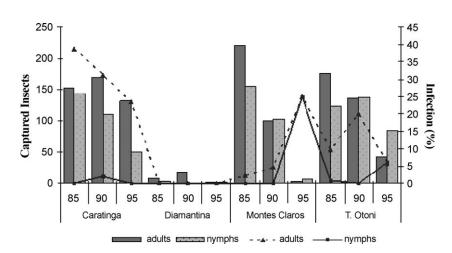


Fig. 3. Number of *T. vitticeps* adults and nymphs captured (columns), and corresponding infection rates (lines), in four sanitary districts of Minas Gerais in 1985, 1990 and 1995.

724 **Table 3**

Mean values (\pm standard deviation) of five variables that best discriminate areas where *T. vitticeps* is present/absent. BIO2: mean daily temperature variation (difference between maximum and minimum temperature); BIO3: daily/annual temperature variation; BIO12: annual precipitation; BIO16: precipitation of most humid trimester; BIO18: precipitation of hottest trimester.

	BIO2	BIO3	BIO12	BIO16	BIO18
Present Absent	12.0 (0.77) 12.6 (0.67)	. ,	1108 (194) 1402 (116)	602.7 (109.6) 734.8 (48.3)	417 (90.4) 601 (110)

26.3% of all triatomines, respectively. When data corresponding to both districts are added (1455), they represent 70.1% of the total capture of *T. vitticeps* by the Control Program during the period (2076 individuals).

Capture data for the four districts, analyzed by species and year, are shown in Table 2. After 1985, when the Control Program recorded its peak of activity (Dias, 2002), T. vitticeps and T. sordida were the least impacted species by control measures. In 1995, these species presented a smaller density reduction when compared to all other. Furthermore, capture data indicate that T. infestans was eliminated from the region during this period. The number of T. vitticeps reported indoors was greatest in the districts of Diamantina, Montes Claros (in the 1980s) and especially in Caratinga (Fig. 2). Peridomiciliary capture of this triatomine was most frequent in Teófilo Otoni and Montes Claros during the 1990s. The infection rate of triatomines captured indoors tended to be greater than that of the insects captured in the peridomicile (Fig. 2). Additionally, adults were more frequently captured than nymphs in most districts (Fig. 3). Particularly at Caratinga, more adults were found infected in comparison to nymphs.

3.2. Spatial analysis

Five of the 20 variables used to perform the analysis were selected in the stepwise discriminant analysis to produce a model that classified sampling sites according to the presence or absence of *T. vitticeps*. Among the variables selected, two variables corresponded to temperature variation and three to rainfall (Table 3). Annual precipitation and precipitation during the most humid trimester were the most important variables for the discrimination of presence/absence of insects (Table 4). This model correctly classified 98.7% and 91.0% of the areas of presence and absence, respectively. The post-classification error was smaller than 4%, i.e., four points corresponding to the presence area were predicted at the absence area and nine points corresponding to the absence of the species.

Table 4

Standardized coefficients of the discriminant functions for canonical variables. BIO2: mean daily temperature variation (difference between maximum and minimum temperature); BIO3: daily/annual temperature variation; BIO12: annual precipitation; BIO16: precipitation of most humid trimester; BIO18: precipitation of hottest trimester. *Most important variables in the discrimination of presence/absence sites.

Variable	Root 1
BIO18	0.84881
BIO3	1.02526
BIO12*	2.29732
BIO16*	-2.05614
BIO2	0.41575
Eigenvalue	2.76035

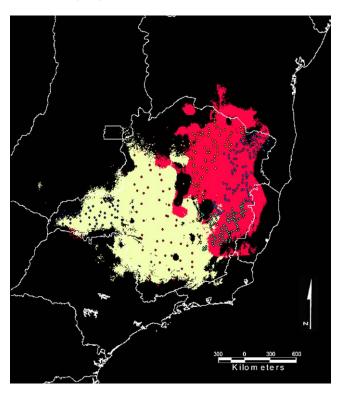


Fig. 4. Areas of presence (red) and absence (yellow) of *T. vitticeps* presented in a classification based on the biophysical variables by discriminant analysis. The green, blue and yellow points within the area of presence refer to the municipalities of Caratinga, Teófilo Otoni and Montes Claros/Diamantina, respectively. The red and blue points within the yellow area represent areas selected randomly for absence of the species. Black areas corresponds to model uncertainty. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

The model built by the stepwise discriminant analysis and the Worldclim data for the five bioclimatic variables were used to produce a map that describes the potential occurrence of *T. vitticeps* (Fig. 4).

3.3. Effect of relative humidity on egg hatching

Hatching of *T. vitticeps* eggs varied from 3 to 95% among the five RH levels (Fig. 5). The results demonstrate that RH interferes dramatically in the hatching rate, with a cut-off point between RH 41–52% ($P \le 0.05$). However, there was no significant difference in the eclosion of eggs between the sectors with RH over 52%. It is worth emphasizing that the maximum eclosion was observed at 100% RH. On the other hand, eggs hardly hatched at the lowest RH (21%).

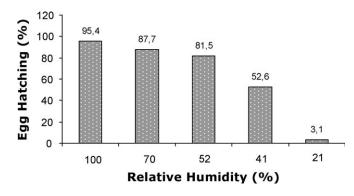


Fig. 5. Influence of relative humidity (RH) on the hatching success of T. vitticeps eggs.

4. Discussion

The ability of a species to invade and colonize man-made environments is directly related to the flying activity and the availability of adequate shelters and food which can be exploited efficiently, respectively. For example, *T. infestans* is the bestadapted triatomine to the indoor conditions, and as a consequence, became the most important vector of *T. cruzi* (Pereira et al., 2006). An effective control program carried out by the PCDCh led to the elimination of the *T. infestans* from almost all of Brazil. However, this also resulted in changes in the behaviour patterns of other triatomine species. Examination of PCDCh records for the area of occurrence of *T. vitticeps* in Minas Gerais revealed that in 1985 *T. infestans* was not recorded at any of the municipalities evaluated.

Silveira et al. (1984) reviewed information from 1975 to 1983, about the domiciliary and peridomiciliary triatomine captures by the control program in all the Brazilian endemic area. In the state of Espírito Santo, 31/36 municipalities (86.1%) were positive for *T. vitticeps* compared to 96/442 (21.7%) in Minas Gerais state and only 1/239 (0.4%) in Bahia state. PCDCh records for Minas Gerais state, related to the 2002–2006 period reveal that *T. vitticeps* was the third captured species (Siloto et al., 2007), after *T. sordida* and *P. megistus*.

The reduction in the number of captured insects was expected, given the extensive campaign using insecticide spraying. However the impact of control measures on *T. vitticeps* and *T. sordida* was smaller than on the other species. This pattern may be related to the biology of these two triatomines. Traditionally, the *T. vitticeps* invades houses and rarely colonizes them. So, the insecticide cannot prevent the invasion of adults, but may protect against the formation of new colonies. In this case, its epidemiological relevance is due to the high infection rates of the invaders. *T. sordida* also occupies predominantly an area represented by the peridomicile, where the insecticide action is very limited, being rapidly degraded (Pires et al., 1999).

T. vitticeps is a Triatominae species with unique characteristics, whose contact with man does not seem to be related to the occurrence of intradomiciliary colonies but rather to repeated invasions of dwellings from surrounding areas (Souza et al., 2008). Although a large number of nymphs were collected in almost all districts, the database used does not discriminate how many adults and nymphs were captured per environment. Thus, we cannot affirm the presence of colonization indoors. Furthermore, as observed in previous studies (Dias et al., 1989; Gonçalves et al., 1998; Souza et al., 2008), the triatomines captured indoors presented higher infection rates than those collected in the peridomicile (Fig. 2), and were principally adult insects (Fig. 3), reinforcing once more the hypothesis of continuous invasion by *T. vitticeps*.

Studies based on remote sensing offer great benefits since they provide historical data for comparison and analysis (Ostfeld et al., 2005). An important application of this tool involves the use of environmental variables, recorded in digital format, to elaborate predictive models of the potential geographical distribution of several vectors of pathogens. Gorla (2002) pioneered the use of environmental variables obtained by means of satellites to propose a predictive map for the distribution of T. infestans, the principal vector of Chagas disease. Recently, Carbajal de La Fuente et al. (2008) also proposed a prediction map for T. wygodzinskyi and T. pseudomaculata, morphologically similar species whose distribution is defined by different environmental characteristics. The variables of temperature and vapor pressure are significant for the presence of T. wygodzinskyi, while for T. pseudomaculata the best discrimination of localities where it is present is related to the vegetation index and ground surface temperature.

The potential distribution map presented here is very similar to the known geographical distribution of *T. vitticeps*. The occurrence of insects in the wild does not necessarily grant their presence in the artificial environment, which depends, as already mentioned, on their capacity to exploit the conditions offered by man-made environments. In the case of *T. vitticeps*, occurrence is reported in houses throughout the natural range of the species demonstrating its ability to invade artificial environments. Although the analysis performed in the present study showed a greater region of occurrence than currently known for the species at Bahia state, it should be taken into account that this region could "potentially" be occupied. The absence of *T. vitticeps* in this area suggests the existence of some physical or climatic barrier that impedes or limits its occupation.

The estimated distribution of T. vitticeps was associated with precipitation and, to a lesser extent, temperature as potential indicators for the occurrence of this vector. Minas Gerais represents an environmental transition zone between three of the most important Brazilian biomes: Atlantic Forest, Cerrado and Caatinga (Scolforo and Carvalho, 2006). In addition, Minas Gerais is the source of important rivers that form five hydrographic basins (São Francisco, Grande, Paranaíba, Doce and Jequitinhonha) and drain about 90% of its area, providing the state with enormous water resources. It has a mountainous landscape, reaching its greatest elevations in the Serra da Mantiqueira and Espinhaço and varying between an elevation of 79 m for the municipality of Aimorés and 2890 m for the Pico da Bandeira, on the border with the Espírito Santo state. The organization of this relief is intimately associated with the great hydrographic basins, including their respective divisions and biomes.

The results obtained by spatial analysis in the theoretical model are clearly coincident with our findings on the egg hatching experiments that showed a strong negative effect of low humidity on eclosion. Only two eggs out of 65 hatched at 21% RH and neither of those nymphs survived. Similar results were observed for P. megistus, where no hatching was observed at 9% RH and only 23% hatching of eggs exposed to 37% RH (Pires, 2003). In a similar way, eggs of Rhodnius prolixus did not hatch at 0% and only 45% of them hatched at 30% RH (Clark, 1935; Schilman, 1998). In contrast, Roca and Lazzari (1994) observed that 94% of T. infestans eggs exposed to 0% humidity hatched. Furthermore, Guarneri et al. (2002) indicate that hatching in T. brasiliensis eggs is lower at extremely low or high humidities. Nevertheless, a significant hatching rate (68.9%) was still observed at 9% RH for T. brasiliensis, indicating that eggs of this species are highly tolerant to desiccation.

Observations carried out with *R. prolixus*, *T. brasiliensis* and *P. megistus*, showed that water saturated environments affect egg hatching negatively, leading the authors to suggest that the development of pathogenic fungi would contribute to reduce eclosion at this RH (Schilman, 1998; Guarneri et al., 2003; Pires, 2003). In contrast to these species, *T. vitticeps* presented the greatest hatching rate at the highest RH tested (95.4%), showing that it is highly tolerant to water saturation. This highlights the importance of this abiotic environmental factor for this vector and reinforces the results obtained with the spatial analysis in the theoretical model using bioclimatic variables.

Acknowledgments

Thanks to Dr. Allaua Saadi for their suggestions. This investigation received financial support from the UNDP/World Bank/WHO Special Programme for Research and Training in Tropical Diseases (TDR), FIOCRUZ (Brazil) and CNPq.

Author's personal copy

R.C.M. de Souza et al. / Infection, Genetics and Evolution 10 (2010) 720-726

References

- Carbajal de La Fuente, A.L., Porcasi, X., Noireau, F., Diotaiuti, L., Gorla, D., 2008. The association between the geographic distribution of Triatoma pseudomaculata and Triatoma wygodzinskyi (Hemiptera: Reduviidae) with environmental variables recorded by remote sensors. Infect. Genet. Evol. 9, 54-61.
- Clark, N., 1935. The effect of temperature and humidity upon the eggs of the bug Rhodnius prolixus (Heteroptera, Reduviidae). J. Anim. Ecol. 4, 82-87.
- Dias, J.C.P., Feitosa, V.R., Ferras Filho, A., Rodrigues, V.L.C., Alencar, S.A., Sessa, P.A., 1989. Fonte alimentar e potencial vetorial do Triatoma vitticeps com relação a doença de Chagas Humana no estado do Espírito Santo, Brasil (Hemiptera, Reduviidae). Mem. Inst. Oswaldo Cruz 84, 165-173.
- Dias, J.C.P., 2002. O controle da doença de Chagas nos países do Cone Sul da América. In: Silveira, A.C. (Ed.), História de uma iniciativa internacional, 1991/2001. Faculdade de Medicina do Triângulo Mineiro, Uberaba, pp. 155-222.
- Dias, J.C.P., 2006. Doença de Chagas: Sucessos e desafios. Cad. Saude Publica 22, 2020–2021.
- Diotaiuti, L., 2007. Triatomíneos. In: Teixeira, A. (Ed.), Doença de Chagas e Evolução. Universidade de Brasília, Finatec, Brasília, pp. 205–231. Dujardin, J.P., 2008. PAD (Permutaciones y Análisis Discriminante). http://
- www.mpl.ird.fr/morphometrics/pad/index.html.
- Gonçalves, T.C.M., Oliveira, E., Dias, L.S., Almeida, M.D., Nogueira, W.O., Pires, F.D.A., 1998. An investigation on the ecology of *Triatoma vitticeps* (Stal, 1859) and its possible role in the transmission of Trypanosoma cruzi, in the locality of Triunfu, Santa Maria Madalena municipal district, state of Rio de Janeiro, Brazil. Mem. Inst. Oswaldo Cruz 93, 711–717.
- Gorla, D.E., Dujardin, J.P., Schofield, C.J., 1997. Biosystematics of old world Triatominae. Acta Trop. 63, 127–140. Gorla, D.E., 2002. Variables ambientales registradas por sensores remotos como
- indicadores de la distribución geográfica de *Triatoma infestans* (Heteroptera: Reduviidae). Ecol. Austral. 12, 117–127.
- Guarneri, A.A., Lazzari, C.R., Diotaiuti, L., Lorenzo, M.G., 2002. The effect of relative humidity on the behaviour and development of Triatoma brasiliensis. Physiol. Entomol. 27, 142-147.
- Guarneri, A.A., Diotaiuti, L., Gontijo, N.F., Gontijo, A.F., Pereira, M.H., 2003. Bloodfeeding performance of nymphs and adults of Triatoma brasiliensis on human hosts. Acta Trop. 87, 361-370.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.
- Lent, H., Wygodzinsky, P., 1979. Revision of the Triatominae (Hemiptera, Reduviidae), and their significance as vectors of Chagas disease. Bull. Am. Mus. Nat. Hist. 163, 127-520.
- Lorosa, E.S., Santos, C.M., Jurberg, J., 2008. Foco de doença de Chagas em São Fidélis, no Estado do Rio de Janeiro. Rev. Soc. Bras. Med. Trop. 4, 419-420.

- Ostfeld, R.S., Glass, G.E., Keesing, F., 2005. Spatial epidemiology: an emerging (or reemerging) discipline. Trends Ecol. Evol. 20, 328-336.
- Pereira, M.H., Gontijo, N.F., Guarneri, A.A., Sant'Anna, M.R.V., Diotaiuti, L., 2006. Competitive displacement in Triatominae: the Triatoma infestans success. Trends Parasitol. 22, 516-520.
- Pires, H.H.R., Borges, E.K., Andrade, R.E., Lorosa, E.S., Diotaiuti, L., 1999. Peridomiciliary infestation with Triatoma sordida Stal, 1859 in the County of Serra do Ramalho, Bahia, Brazil. Mem. Inst. Oswaldo Cruz 94, 147-149.
- Pires, H.H.R., 2003. Ecologia comparativa de Panstrongylus megistus (Burmeister, 1835) (Hemiptera: Reduviidae) em laboratório [Tese]. Universidade Federal de Minas Gerais. Belo Horizonte.
- Roca, M.J., Lazzari, C.R., 1994. Effects of relative humidity on the Haematophagous bug Triatoma infestans: hygropreference and eclosion success. J. Insect Physiol. 40, 901-907.
- Santos, U.M., Pinto, A.F.S., Almeida, A.Z., 1969. Doença de Chagas no Espírito Santo. III. Vetores do Trypanosoma. Rev. Soc. Bras. Med. Trop. 1, 51-52.
- Santos, C.B., Leite, G.R., Sessa, P.A., Falqueto, A., 2006. Dynamics of feeding and defecation in *Triatoma vitticeps* (Stal, 1859) (Hemiptera, Reduviidae, Triatominae) and its potential in the transmission of Trypanosoma cruzi. Mem. Inst. Oswaldo Cruz 101, 543-546.
- Schilman, P.E., 1998. Factores que afectan la reproducción de las vinchucas: aspectos fisiológicos y comportamentales [Tese]. Universidad de Buenos Aires, Buenos Aires.
- Schofield, C.J., Galvão, C., 2009. Classification, evolution, and species groups within the Triatominae. Acta Trop. 110, 88-100.
- Scolforo, J.R., Carvalho, L.M.T., 2006. Mapeamento e inventário da flora nativa e dos reflorestamentos de Minas Gerais. Universidade Federal de Lavras, Lavras, 288
- Sessa, P.A., Carias, V.D.R., 1986. Infecção natural de triatomíneos do Espírito Santo por Flagelados morfologicamente semelhantes ao Trypanosoma cruzi. Rev. Soc. Bras. Med. Trop. 19, 99–100.
- Siloto, H.H., Diotaiuti, L., Azeredo, B.V.M., 2007. Distribuição da fauna triatomínica, segundo o Programa de Controle da Doença de Chagas (PCDCH), no Estado de Minas Gerais, no período de 2002 a 2006. In: XXIII Reunião de Pesquisa Aplicada em Doença de Chagas e Leishmanioses, Anais, 25 a 27 de outubro, Uberaba, MG, Brasil.
- Silveira, A.C., Feitosa, V.R., Borges, R., 1984. Distribuição de triatomíneos capturados no ambiente domiciliar, no período 1975-1983, Brasil. Rev. Bras. Mal. Doencas Trop. 36, 15-312.
- Souza, R.C.M., Barbosa, S.E., Sonoda, I.V., Azeredo, B.V.M., Romanha, A.J., Diotaiuti, L., 2008. Population dynamics of Triatoma vitticeps (Stål, 1859) in Itanhomi, Minas Gerais, Brazil. Mem. Inst. Oswaldo Cruz 103, 14-20.
- WHO World Health Organization, 1990. Potential health effects of climatic change. Geneva, 58 pp.

726