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Feeding and Defecation Patterns of *Rhodnius nasutus* (Hemiptera; Reduviidae), A Triatomine Native to an Area Endemic for Chagas Disease in the State of Ceará, Brazil

Tiago G. Oliveira, Filipe A. Carvalho-Costa, Otília Sarquis, and Marli M. Lima*
Laboratório de Eco-Epidemiologia da Doença de Chagas, Laboratório de Sistemática Bioquímica, Instituto Oswaldo Cruz, Fundação Oswaldo Cruz, Rio de Janeiro, Brazil

Abstract. The importance of *Rhodnius nasutus* in the transmission of Chagas disease in northeastern Brazil was investigated regarding feeding and defecation patterns of this triatomine under laboratory conditions. An average of 30 samples were studied for each instar, from fourth-instar nymphs onward. On average, 86.4% started feeding after less than 10 minutes. In terms of the duration of feeding, 53.3% of fourth instar nymphs, 81.9% of fifth-instar nymphs, 21.9% of males, and 36.7% of females fed for more than 15 minutes. In all groups, there were insects that defecated and urinated during feeding; adult males defecated the most and fourth instar nymphs defecated the least. The results demonstrate that *R. nasutus* may be considered an efficient *T. cruzi* vector because it avidly searches for a food source, has a lengthy feeding time with low probability of interruption during feeding, and achieves a high percentage of engorgement.

INTRODUCTION

Chagas disease, or American trypanosomiasis, is caused by the protozoan *Trypanosoma cruzi* and is endemic in rural poor populations that live in homes in which triatomines can easily enter and settle.[1] These insects are obligatorily hematophagous in all phases of their life cycle and are therefore susceptible to *T. cruzi* infection during all instar stages. However, because of differences in biologic and ecologic characteristics, only a limited number of species can cause the transmission of Chagas disease to humans.[2,3] The genus *Rhodnius* is one of the most important transmitters of Chagas disease because it comprises some of the main trypanosomiasis vectors, including *Rhodnius prolixus*. Palm trees are natural ecotopes of the *Rhodnius* species and may be considered ecologic indicators of risk areas for Chagas disease.[4–6]

Rhodnius nasutus (Stal 1859) is a wild species[7] that is widespread in the semi-arid environments (Caatinga) of northeastern Brazil,[2,8] where it inhabits the crowns of palm trees and bird nests.[5,8–10] In the natural habitat, its feeding preference is for birds and opossums.[9]

This species, when compared with other native *Rhodnius* species in northeastern Brazil, exhibits a greater capacity for spreading.[11] Recent studies carried out in the state of Ceará indicate that besides being frequently captured in carnauba palms (*Copernicia prunifera*), *R. nasutus* has also been captured in oiticica (*Licania rigida*), a typical tree in the Caatinga (Brazilian scrublands) that belongs to the family Chrysobalanaceae.[12] This finding indicates that its habitat is not restricted to palm trees. In Caatinga, *R. nasutus* colonizes the peridomiciliar environment, mainly in hen houses and goat/sheep corrals. Adult insects are frequently collected inside homes, although intradomicile colonies have not yet been found. Among these environments, the captured samples almost always harbored *T. cruzi* with an infection level more than 15%, therefore presenting a risk for humans.[9,10,13–16]

Recently, in addition to *T. cruzi*, *T. rangeli* was encountered for the first time in *R. nasutus* in the state of Ceará, with a natural infection rate of 7.7%.[9] In a recent survey conducted in Jaguaruana, Ceará, *R. nasutus* infected with *T. cruzi* were collected in intradomiciliar and peridomiciliar environments.[17]

The genus *Rhodnius* is known for its voracity in searching for food[18] and for ingesting a high volume of blood during feeding. Considering that the time that triatomine insects take to defecate is a crucial factor in the transmission of *T. cruzi*,[19,20] the present study investigated the feeding and defecation patterns of *R. nasutus* with the goal of estimating its potential capacity for transmitting Chagas disease in northeastern Brazil.

MATERIALS AND METHODS

Rhodnius nasutus insects used in this study were part of the third generation of a colony that was originally from periurban areas of Jaguaruana, a small city located in the Jaguaribe Valley in the eastern region of the state of Ceará. Third-instar nymphs were fed on a pigeon every two weeks and were kept at room temperature until ecdysis to the following instar stage. On average, 30 samples of each instar were observed, starting with fourth-instar nymphs and continuing until the occurrence of male and female differentiation, resulting in a total of 125 specimens.

Observations were carried out between the seventh and ninth days after ecdysis, the period in which the insects were deprived of food. *Rhodnius nasutus* specimens were individually identified[21] and placed into transparent glass vials that were covered with a nylon screen and contained folded filter paper to facilitate the insects' movement and enable contact with the food source.

A pigeon with a previously plucked flank was anesthetized with a mixture of ketamine (20 mg/kg) and xilazina (2 mg/kg) and placed over the glass vials where the behavior of the triatomines was monitored. This procedure was reviewed and approved by the Animal Use and Care Committee of the Oswaldo Cruz Foundation (license no. L-0064/08). A 90-minute period was allotted for each observation and the following variables were assessed: host-contacting time, feeding time, index feeding time/host-contacting time, number of interruptions during feeding, percentage of engorged insects, and percentage of insects that excreted feces during or up to 10 minutes after feeding.

The host-contacting time was defined as the interval from the moment when food was offered to the moment when the insect had its mouthparts inserted into the pigeon's skin.

*Address correspondence to Marli M. Lima, Laboratório de Eco-Epidemiologia da Doença de Chagas, Instituto Oswaldo Cruz, Fiocruz. Av. Brasil, 4365, 21045-900, Rio de Janeiro/RJ, Brazil. E-mail: mmlima@ioc.fiocruz.br

The feeding time was defined as the interval from the first bite to the moment when the insect abandoned the food source. An insect was considered fully engorged when it became completely replete with blood, changing clearly its shape through abdominal stretching.

Observations were carried out between 10:00 AM and 4:00 PM in natural light and at room temperature. Temperature and humidity were recorded with a Fisher Scientific thermohygrometer (Fisher Scientific, Pittsburgh, PA) and were 29.5 ± 3.5°C and 63.5 ± 9.2%, respectively. Statistical analyses were carried out using the Kruskal-Wallis, Fisher's exact, and chi-square tests with the BioEstat (Instituto de Desenvolvimento Sustentável Mamirauá (IDSM), Tefé, AM) and Epi Info (Centers for Disease Control and Prevention, Atlanta, GA) statistical programs.

RESULTS

Host-contacting time. A high percentage (86.4%) of the 125 triatomines studied took less than 10 minutes to start moving towards the food source. Males started feeding more quickly, followed by females and fifth-instar nymphs. The fourth-instar nymphs took longer between movement and feeding (Figure 1), but the difference was not statistically significant ($P = 0.369$).

Feeding time. After reaching the food source, 60% of fourth-instar nymphs, 87.8% of fifth-instar nymphs, 25% of males, and 43.3% of females took more than 15 minutes to feed. As shown in Figure 2, males and females showed a statistically significant lower feeding time than fifth-instar nymphs ($P < 0.001$). Males showed a lower feeding time than fourth-instar nymphs ($P < 0.001$).

Index feeding time/host-contacting time. This index relates the time the insect takes to feed, and thus became in contact with the host, and the time it takes to contact the host, which reflects avidity by the blood source. The fifth-instar nymphs showed the highest index, but the difference was not statistically significant ($P = 0.089$) (Figure 3).

Number of interruptions. Once engorgement started, most of the triatomines continued with no interruption until reaching repletion. Females showed greater continuity when eating because only 3 of 30 had any interruptions. The number of feeding interruptions for fourth-instar nymphs, fifth-instar nymphs, and males ranged from one to four times ($P = 0.374$) (Table 1).

Excrement elimination during and directly after feeding. Of 125 triatomines tested, 72 (57.6%) defecated while feeding. Of these triatomines, 45 (62.5%) defecated more than once. As shown in Table 2, the highest percentage of defecation during feeding was in adult males (75%, 95% confidence interval [CI] = 56.6–88.5%) and the lowest was for fourth-instar nymphs (46.7%, 95% CI = 28.3–65.7%). However, there was no statistically significant difference ($P = 0.085$). We observed

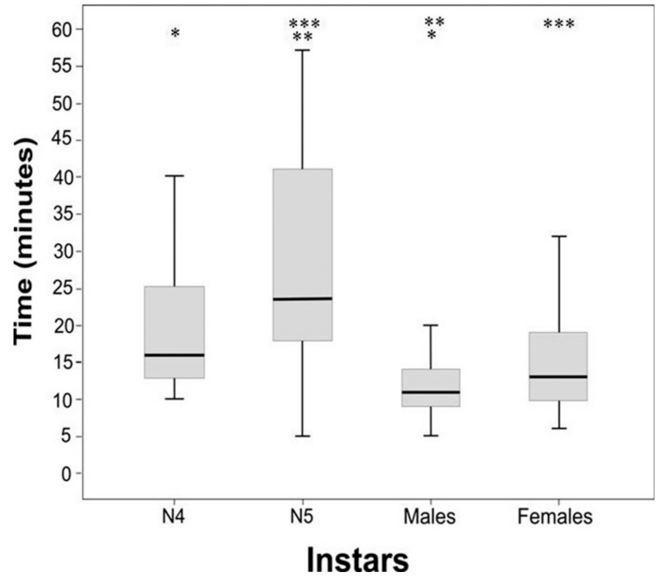

FIGURE 2. Box plots representing medians and interquartile intervals of the feeding time for different instars of *Rhodnius nasutus*, Ceará, Brazil. *, **, and *** Significant differences between groups ($P < 0.05$, by Kruskal-Wallis test).

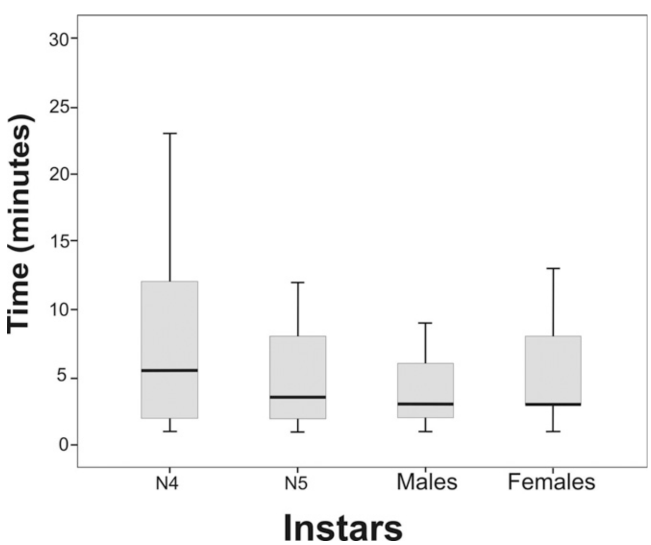

FIGURE 1. Box plots representing medians and interquartile intervals of the host-contacting time for different instar stages of *Rhodnius nasutus*, Ceará, Brazil.

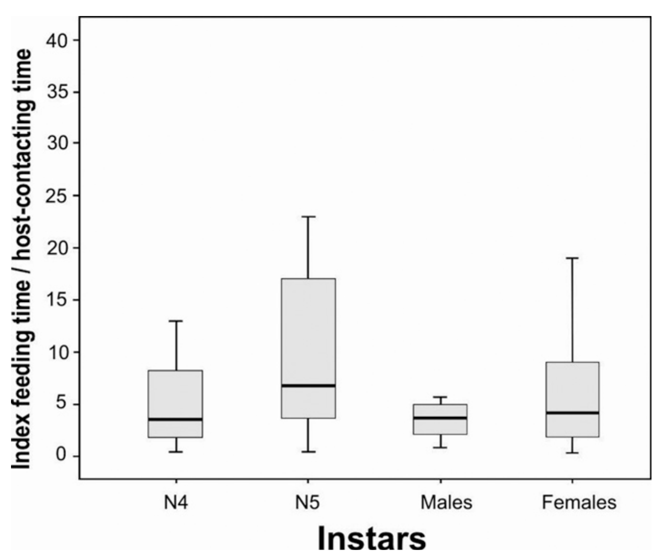

FIGURE 3. Box plots representing medians and interquartile intervals of the index feeding time/host-contacting time for different instars of *Rhodnius nasutus*, Ceará, Brazil.

TABLE 1
Number of feeding interruptions in different *Rhodnius nasutus* instars, Ceará, Brazil

Instar	No. triatomines sampled	No. (%) feeding interruptions				
		0	1	2	3	4
Fourth	30	23 (76.6)	5 (16.6)	0	0	2 (6.6)
Fifth	33	25 (75.7)	6 (20)	0	1 (10%)	1 (3)
Males	32	23 (71.9)	7 (21.9)	1 (3.1)	0	1 (3.1)
Females	30	27 (90)	3 (10)	0	0	0

that within 10 minutes after feeding, 62.5% (95% CI = 43.7–78.9%) of males and 24.2% (95% CI = 11.1–42.3%) of fifth-instar nymphs had eliminated excrement ($P = 0.018$).

Percentage of insects that became engorged after feeding. A total of 90.4% of triatomines were completely engorged after feeding. The highest proportion of engorgement was observed among fifth-instar nymphs (97%) and the lowest was among males (75%) ($P = 0.007$) (Table 2).

DISCUSSION

Information on the feeding and defecation patterns of Triatominae is relevant to the epidemiology of Chagas disease because it is indicative of the species' capacity as a vector for *T. cruzi* transmission. Despite the potential importance of *R. nasutus* in the epidemiology of this disease in northeastern Brazil, especially in the state of Ceará, no studies have been conducted to assess its actual capacity for *T. cruzi* transmission. In this regard, some variables related to the feeding and defecation behavior of triatomines are important in evaluating their potential as vectors. Among these behavioral variables, the time elapsed between the offering of the food source and the initiation of feeding (host-contacting time) denotes to some extent the avidity of the insects for the blood source, which is a prerequisite for transmission of *T. cruzi* infection.

We observed that after the food source was made available, *R. nasutus* specimens took a median of 15 minutes (range = 5–76 minutes) to start feeding. Differences between the various instars were not significant. The average time to feeding was previously reported to be four and five minutes for *R. prolixus* and *R. pictipes* feeding on mice and pigeons, respectively.[22,23] Moreover, most *R. neiva*, *R. prolixus*, and *R. robustus* took less than three minutes to start feeding on artificial feeders filled with human blood.[24] Despite the differences in the methods used in these experiments with regard to the food source and other laboratory conditions, we suggest that *R. nasutus*, like other *Rhodnius* species, shows good avidity and voracity for the blood source and rapid initiation of feeding.

The pigeons used had not previously served as a food source for the insects. This ensured that there was no possibility of them being contaminated with *R. nasutus* saliva because it has been suggested that previous exposure to triatomine saliva results in a shortened host-contacting time for feeding.[25]

With regard to the feeding time, increased contact time with the food source should create a greater chance of eliminating feces on the host.[26] The time spent to engorge could also constitute an epidemiologically relevant variable when the source is infected because the longer the triatomine spends engorging, the greater the chance for parasite ingestion,[17] although the chance of a feeding interruption also increases because of host movement. In our observations, the average feeding time of *R. nasutus* was 20 minutes to reach engorgement. It was reported that species that are epidemiologically important in the transmission of Chagas disease had long feeding times: 17, 21, and 30 minutes for *R. prolixus*, *Triatoma infestans,* and *Triatoma dimidiata,* respectively.[27] Nevertheless, some insects took 4–10 minutes to engorge.[22]

Interruptions during feeding also represent an important behavioral characteristic with regard to *T. cruzi* transmission by triatomines. In this context, species that show continuous feeding have a longer contact period with the host and may be considered more efficient vectors. We observed that although most individuals did not show any interruptions during feeding, few *R. nasutus* specimens in all instars had interruptions, as observed in other triatomine species. In previous studies, other investigators[28] reported interruptions in all *R. colombiensis* and *R. prolixus* instars except for *R. colombiensis* first instars, in which none of the specimens interrupted their feeding. Also, although most *Triatoma rubrofasciata* nymphs did not interrupt their feeding, few interruptions were observed for all studied instars.[29] Similar findings were observed in our study: *R. nasutus* tended to show continuous feeding, and only 20% of specimens had interrupted feeding.

Because *T. cruzi* is transmitted by feces, triatomines that defecate during feeding or a short time after repast are of great importance in the transmission of Chagas disease. In our study, a high percentage of *R. nasutus* defecated during or directly after feeding. This data also indicates the capacity of the genus *Rhodnius* to be a vector for *T. cruzi* transmission, as has also been observed by other investigators.[23,30–32] It was observed that of six triatomines species studied,[33] 50% of *R. prolixus* specimens defecated during or soon after repast. The authors argued that on the basis of defecation behav-

TABLE 2
Rates of defecation during and after feeding, and engorgement in different instars of *Rhodnius nasutus*, Ceará, Brazil*

Instar	Defecation				Engorgement	
	During feeding		After feeding			
	Observed/total (%)	95% CI	Observed/total (%)	95% CI	No. (%)	95% CI
Fourth	14/30 (46.7)	28.3–65.7†	15/30 (50)	31.3–68.7†	28 (93.3)	77.9–99.2
Fifth	16/33 (48.5)	30.8–66.5†	8/33 (24.2)	11.1–42.3†	32 (97)	84.2–99.9‡
Males	24/32 (75)	56.6–88.5†	20/32 (62.5)	43.7–78.9†	24 (75)	56.6–88.5‡§
Females	18 /30 (60)	40.6–77.3	13/30 (43.3)	25.5–62.6	29 (96.7)	82.8–99.9§
Total	72/125 (57.6)	48.4–66.4	56/125 (44.8)	35.9–54	113 (90.4)	83.8–94.9

* CI = confidence interval.
† $P < 0.05$, by chi-square test.
‡ $P = 0.012$.
§ $P = 0.026$, by two-tailed Fisher's exact test.

ior, *R. prolixus* could be the most efficient vector for *T. cruzi* transmission among all species studied. Also, it was shown that *R. prolixus* had the greatest defecation index in nearly all instars when compared with *T. dimidiata* and *T. infestans*.[22] With regard to other genera of Triatominae, 73% of *Triatoma patagonica* specimens defecated within 30 minutes after feeding.[34] It was also demonstrated that *Triatoma rubrovaria* defecated frequently during and after feeding,[35] whereas *T. rubrofasciata* defecated little during feeding.[29]

To compare the vector potential of different instars of *R. nasutus,* we evaluated the behavioral variables of host-contacting time, feeding time, index feeding time/host-contacting time, and rate of defecation. With regard to the host-contacting time, adult males started feeding more quickly. Nevertheless, fifth-instar nymphs showed the longest feeding time, being the slowest to engorge. We observed that fifth-instar nymphs tended to show the highest index, combining a shorter time to the initiation of feeding with a longer time in contact with the host, but this was not statistically significant. With regard to the rate of insects that were engorged after feeding, we found that the highest proportion of engorgement was observed among fifth-instar nymphs and the lowest was among males. However, with respect to the defecation pattern, fifth-instar nymphs had a rate of defecation significantly lower than that of adult males. It was reported that *R. prolixus* and *R. colombiensis* fifth-instar nymphs have a longer feeding time than other instars.[22,28] It has been proposed that the longer feeding time observed for fifth-instar nymphs may be related to a greater food requirement because of the acquisition of new anatomic structures during molting to the adult stage.[28]

The results obtained in this study might have been different with a mammal or an artificial feeder as the food source because the host may influence feeding patterns in triatomines. A study analyzing four species of the *R. prolixus* complex, including *R. nasutus*, found distinct feeding behaviors with different hosts (artificial feeder, pigeon, and mouse).[36] These results suggested that *R. nasutus* was the most effective species in obtaining blood from mice. However, this species had a quicker host-contacting time than the other species when feeding on pigeons (*R. nasutus* < *R. prolixus* < *R. neglectus* < *R. robustus*). The average number of non-ingestive events was usually higher on mice than on pigeons for all species except *R. nasutus*. In terms of cumulative host-contact time, the quickest species when feeding on pigeons were *R. prolixus and R. neglectus* < *R. nasutus* < *R. robustus*. The authors argued that differences among these species might be related to distinct salivary adaptations to each host and implied that *R. nasutus* may be well-adapted to feed on mice.[36]

Regarding other triatomine species, a study comparing the feeding behavior of *Triatoma infestans, Triatoma brasiliensis,* and *Triatoma pseudomaculata* showed that the rate of engorgement tended to be greater on pigeons than on mice in all three species. With mice, host-contacting time tended to be longer, with more prolonged interruptions, reinforcing the conjecture that feeding on mice is more difficult than feeding on pigeons and requires more contact time to obtain a similar quantity of blood.[37]

Chagas disease is endemic in Caatinga,[8,38] where *R. nasutus* has been commonly found in domiciliary units along with *Triatoma brasiliensis* and *Triatoma pseudomaculata*. These are autochthonous species and are thus more difficult to control. Additionally, they commonly show high indices of *T. cruzi* infection when captured in their natural habitats.

Before successful *Triatoma infestans* control in the Southern Cone countries of South America, wild or semi-wild triatomines aroused little attention because they were restricted to their wild environments. Currently, sylvatic triatomines have drawn the attention of public health authorities because these insects have invaded domiciles and peridomiciles in rural and peri-urban zones of disease-endemic regions, which is probably a consequence of deforestation and alterations in their natural ecotopes.[10] This finding became more evident after the effective control of *Triatoma infestans* was achieved in countries where this triatomine was the main vector of Chagas disease. Such a change in the epidemiologic scenario has encouraged authorities to realize the importance of secondary vector species for the success of control of disease in disease-endemic areas. In this context, understanding biologic aspects such as the life cycle, reproduction, feeding, and defecation patterns, as well as the capacity for invasion and colonization of artificial ecotopes, is of great importance in planning of control programs in disease-endemic areas. Understanding these various factors clarifies the risks posed by these species with regard to *T. cruzi* transmission.

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Authors' addresses: Tiago G. Oliveira, Otília Sarquis, and Marli M. Lima, Laboratório de Eco-Epidemiologia da Doença de Chagas, IOC, FIOCRUZ, Av. Brasil, 4365, Rio de Janeiro, RJ, Brazil, CEP 21045-900, E-mails: tiago@ioc.fiocruz.br, otiliasarquis@ioc.fiocruz.br, and mmlima@ioc.fiocruz.br. Filipe Anibal Carvalho-Costa, Laboratório de Sistemática Bioquímica, Instituto Oswaldo Cruz, Fundação Oswaldo Cruz, Rio de Janeiro, Brazil, CEP 21045-900, E-mail: guaratiba@ioc.fiocruz.br.

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