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Observations on the feeding and defecation patterns of three triatomine species (Hemiptera: Reduviidae)

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Summary

A comparative laboratory study of feeding and defecation behavior of three species of triatomines (*Rhodnius prolixus, Triatoma infestans* and *T. dimidiata*) indicated evident differences among the species and among the different stages of same species. Time required for a full blood meal was related to the size of the specimen. Insects required an average of 11–28 min for engorgement although some finished within 10 min. *T. dimidiata* frequently interrupted the act of feeding, a probable explanation of the higher number of defecations before finishing a blood meal observed in this species. *R. prolixus* was superior to the other two species in number of defecating insects and in rapidity and frequency of defecations within a given time. *T. dimidiata* was inferior in all three parameters and *T. infestans* was intermediate. Males of all species tended to be less effective. A "defecation index" is proposed for comparing this different behavior in triatomine specimens under standard conditions.

Effectivity of the insects according to the measured parameters is discussed in relation to the prevalence of Chagas' disease in those areas where they are principal vectors.

Introduction

Behavioral studies on the attack, time of feeding and defecation time of triatomes is of great importance for a better understanding of the transmission of *Trypanosoma (Schizotrypanum) cruzi.* Wood (1951) was the first to observe that some North American species do not defecate during the blood meal or even immediately after, while Dias (1956) demonstrated that South American species were more "efficient" in this respect. These differences in the effectivity of transmission of the parasite by some species could explain, at least in part, the

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greater prevalence of Chagas' disease in certain areas of the American continent.

The purpose of this study was to measure the feeding and defecation behavior under experimental conditions of both nymphs and adults of three important vectors of the disease.

Material and methods

The insects were from three of our laboratory colonies as follows: *R. prolixus* originally from El Salvador, *T. infestans* from Chile, and *T. dimidiata* from Costa Rica. For each of the three species of insects, a total of 210 (30 each of the five nymphs instars and male and female adults) were fed to repletion on C3H mice; in each experiment, 3–6 insects were placed with one mouse. These insects had been fasting for periods of not less than two weeks and the most avid biters (biting at an extended finger) were selected. An identifying number was painted on the back of each insect with white paint; for the smallest nymphs, marks on different legs were used. The mouse was put in a 150×50 mm transparent plastic container and was restrained with masking tape tight enough to prevent violent movements. The insects were left in the container for 60–150 min, in a slightly darkened room with mean maximum and minimum temperatures of 22.9 and 21.1° C. The insects were observed continuously by the same observer and the container was not moved or disturbed during the experiment. Insects that did not feed avidly were disregarded and replaced in subsequent experiments.

For each insect a chronometer record was made of the time of initiation of its attack on the mouse, of withdrawal and of each new feeding; also of the time of each defecation and whether during or after feeding.

Results and conclusions

Data on duration of feeding by the insects are shown in Tables 1–3 and those of defecation in Tables 4–6. From these tables we can deduce that usually the different hungry instars of the three species attack their victims soon after exposure, with the exception of the smaller nymphs of *T. dimidiata,* some of which may take up to an hour or more.

In general, within the same species, duration of feeding was in direct relation to the size of the corresponding nymphal instar. The females usually took longer than the males but fed for shorter periods than the larger nymphs. The same ratios of size and time were also seen within the different species: *T. dimidiata* is larger than *T. infestans* which is larger than *R. prolixus.* All the insects required an average of 11–28 min to become completely engorged, with the exception of the 5th instar nymphs and adults of *T. dimidiata,* which required longer. However, interruptions during feeding are included in the overall time and therefore the more interruptions there were, the longer the elapsed time. Interruptions during feeding were made by 39% of the *T. dimidiata;* some insects withdrew from the victim as many as 6 times and took considerable time in resuming feeding. On the other hand, with only two exceptions some insects of all stages of the three species took a full meal in less than 10 min.

Table 1. Engorging period for *T. dimidiata* on a restrained mouse. Information based on 30 insects of each instar in 6–11 experiments for each instar

Instar	Mean time for starting a blood meal (range)	Mean time for engorging (range)	No. of insects that interrupted the blood meal (%)	Total No. of interruptions	Mean No. of interruptions per insect (range)
1st	18:10* (0–66:50)	21:39 (9:35–41:55)	3 (10.0)	3	0.10 (0–1)
2nd	13:55 (0–48:55)	15:41 (4:00–34:05)	14 (46.7)	22	0.73 (0–3)
3rd	4:05 (0–43:40)	24:59 (6:30–62:45)	22 (73.3)	38	1.27 (0–6)
4th	7:30 (0–75:30)	25:19 (9:35–68:35)	14 (46.7)	28	0.93 (0–6)
5th	3:20 (0–16:00)	53:18 (5:45–131:30)	12 (40.0)	9	0.30 (0–2)
Female	3:30 (0–29:55)	40:59 (13:15–79:25)	7 (13.3)	11	0.37 (0–3)
Male	3:50 (0–26:30)	32:42 (7:50–63:05)	10 (33.3)	29	0.97 (0–6)
Mean or mean of means	7:46	30:40	11.7 (39.0)	20.9	0.67

* minutes:seconds

Defecation patterns showed that some specimens of *T. dimidiata* in all instars tended to defecate before finishing a blood meal, a behavior that seems to be related to the frequent interruptions and longer over-all feeding time of this species. It occurred also in some instars of *R. prolixus* but rarely in *T. infestans.* Among those insects delaying the first defecation until after the blood meal, the average time elapsed was 3–4 times longer in *T. dimidiata*, especially in the males and first instars. *T. infestans* was much faster than *T. dimidiata* and uniform in all instars except the first which took longer than the others. *R. prolixus* nymphs were the fastest of the three species especially the second and third instars; adults, especially the males, were slower than those of *T. infestans.* The number of insects which defecated during the first 10 min is smaller in *T. dimidiata* as compared with the other two species, as was also, in general, the number of accumulated defecations. *T. infestans* and *R. prolixus* were more efficient in both parameters; in the latter, all stages surpassed notably the other species in numbers of defecations per insect in this time period, with the exception of the adult males which, as noted above, were slower to begin defecation. After an hour practically all the *T. infestans* and *R. prolixus* had defecated but some of the *T. dimidiata* nymphs had failed to do so. Again, the efficiency of *R.*

Table 2. Engorging period for *T. infestans* on a restrained mouse. Conditions as in Table 1

Instar	Mean time for starting a blood meal (range)	Mean time for engorging (range)	No. of insects that interrupted the blood meal (%)	Total No. of interruptions	Mean No. of interruptions per insect (range)
1st	3:50 (0–31:30)	14:30 (6:45–28:20)	10 (33.3)	14	0.46 (0–5)
2nd	2:55 (0–24:20)	12:19 (3:25–21:10)	1 (3.3)	1	0.03 (0–1)
3rd	6:05 (0–24:15)	16:09 (6:20–32:15)	6 (20.0)	7	0.23 (0–2)
4th	2:10 (0–6:10)	26:03 (7:50–69:25)	8 (26.7)	11	0.36 (0–3)
5th	3:25 (0–10:50)	27:45 (10:00–52:30)	7 (23.3)	11	0.36 (0–4)
Female	3:10 (0–21:35)	25:54 (8:55–41:30)	0	0	0
Male	3:50 (0–19:30)	28:04 (10:40–51:25)	0	0	0
Mean or mean of means	3:38	21:32	4.6 (15.3)	6.3	0.21

Table 3. Engorging period for *R. prolixus* on a restrained mouse. Conditions as in Table 1

Instar	Mean time for starting a blood meal (range)	Mean time for engorging (range)	No. of insects that interrupted the blood meal (%)	Total No. of interruptions	Mean No. of interruptions per insect (range)
1st	2:30 (0–26:40)	11:30 (6:05–28:20)	3 (10.0)	3	0.10 (0–1)
2nd	1:35 (0–20:40)	13:46 (5:40–22:00)	1 (3.3)	1	0.03 (0–1)
3rd	1:40 (0–8:15)	16:36 (8:20–44:50)	1 (3.3)	1	0.03 (0–1)
4th	6:55 (0–17:00)	20:13 (9:45–46:40)	2 (6.7)	2	0.06 (0–1)
5th	5:35 (0–52:00)	26:42 (14:25–49:55)	4 (13.3)	6	0.20 (0–2)
Female	5:50 (0–42:50)	18:47 (6:00–40:30)	3 (10.0)	5	0.16 (0–2)
Male	4:10 (0–16:40)	14:26 (3:30–38:35)	2 (6.7)	3	0.10 (0–2)
Mean or mean of means	4:02	17:26	2.3 (7.6)	3.0	0.10

Table 4. Characteristics of the defecation pattern of *T. dimidiata* fed on a restrained mouse. Conditions as in Table 1

Instar	No. of insects that defecated before finishing the blood meal	Mean time for defecation after the blood meal (range)	No. of insects that defecated up to the first 10 min (%)	Mean of defecations per insect during the first 10 min	No. of insects that defecated up to the first hour (%)	Mean of defecations per insect during the first hour (range)
1st	1	17:00 (0:20–56:45)	13 (43.3)	0.5	23 (76.6)	1.6 (0–5)
2nd	3	6:39 (0:05–38:10)	20 (66.6)	0.8	26 (86.7)	1.6 (0–7)
3rd	4	7:27 (0:15–52:45)	21 (70.0)	0.8	24 (80.0)	2.0 (0–4)
4th	4	11:15 (0:15–53:50)	20 (66.6)	1.1	28 (93.3)	3.3 (1–8)
5th	3	9:44 (0:05–45:25)	23 (76.6)	1.6	29 (96.7)	2.5 (1–6)
Female	9	11:35 (0:05–58:25)	22 (73.3)	1.2	30 (100)	3.4 (1–8)
Male	4	16:15 (0:20–54:20)	13 (43.3)	0.5	30 (100)	1.5 (1–4)
Mean or mean of means	4.0	11:25	18.9 (62.9)	0.9	27.1 (90.5)	2.3

Table 5. Characteristics of the defecation pattern of *T. infestans* fed on a restrained mouse. Conditions as in Table 1

Instar	No. of insects that defecated before finishing the blood meal	Mean time for defecation after the blood meal (range)	No. of insects that defecated up to the first 10 min (%)	Mean of defecations per insect during the first 10 min	No. of insects that defecated up to the first hour (%)	Mean of defecations per insect during the first hour (range)
1st	1	6:34 (0:20–28:20)	21 (70.0)	1.3	30 (100)	5.8 (3–12)
2nd	0	3:54 (0:30–26:40)	26 (86.7)	1.2	30 (100)	6.6 (3–12)
3rd	0	2:50 (0:05–8:35)	28 (93.3)	1.5	30 (100)	6.8 (4–11)
4th	0	3:52 (0:05–15:30)	24 (80.0)	1.6	30 (100)	6.2 (3–11)
5th	1	3:35 (0:15–13:55)	27 (90.0)	1.3	30 (100)	4.4 (2–9)
Female	0	2:44 (0:05–19:35)	28 (93.3)	1.1	30 (100)	3.0 (1–6)
Male	0	3:17 (0:15–10:10)	26 (86.7)	1.0	27 (90.0)	1.8 (1–5)
Mean or mean of means	0.3	3:49	25.7 (85.7)	1.3	29.6 (98.6)	4.9

Table 6. Characteristics of the defecation pattern of *R. prolixus* fed on a restrained mouse. Conditions as in Table 1

Instar	No. of insects that defecated before finishing the blood meal	Mean time for defecation after the blood meal (range)	No. of insects that defecated up to the first 10 min (%)	Mean of defecations per insect during the first 10 min	No. of insects that defecated up to the first hour (%)	Mean of defecations per insect during the first hour (range)
1st	0	2:05 (0:05–13:10)	28 (93.3)	2.5	30 (100)	11.8 (4–20)
2nd	4	0:24 (0:05–2:25)	29 (96.7)	3.6	30 (100)	16.2 (9–28)
3rd	4	0:42 (0:05–8:10)	29 (96.7)	2.8	30 (100)	12.3 (7–28)
4th	5	1:02 (0:05–5:10)	30 (100)	3.8	30 (100)	14.6 (10–26)
5th	3	1:17 (0:05–10:05)	29 (96.7)	1.9	30 (100)	9.6 (4–21)
Female	0	4:41 (0:05–53:35)	26 (86.7)	1.7	30 (100)	7.4 (1–17)
Male	0	12:31 (0:05–38:00)	17 (56.7)	0.9	29 (96.7)	4.8 (1–13)
Mean or mean of means	2.3	3:15	26.9 (89.5)	2.5	29.9 (99.5)	11.0

Table 7. Defecation indices for three species of triatomines

Instar or sex	*T. dimidiata*	*T. infestans*	*R. prolixus*
1st	0.2	0.9	2.3
2nd	0.5	1.0	3.5
3rd	0.6	1.4	2.7
4th	0.7	1.3	3.8
5th	1.2	1.2	1.8
Females	0.9	1.0	1.5
Males	0.2	0.9	0.5

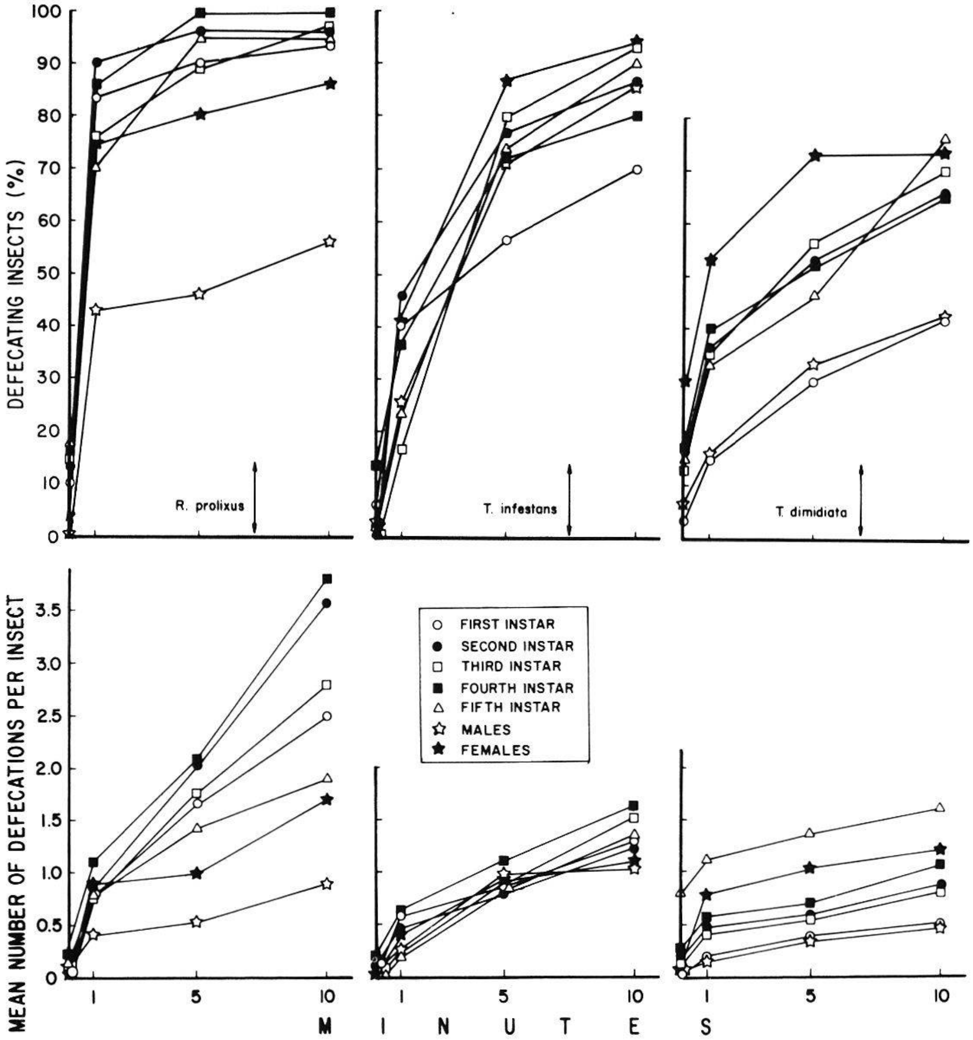

Fig. 1. Percentage of defecating triatomines and mean cumulative number of defecations per insect in a period of 10 min, by instar and sex (30 individuals in each class).

prolixus in producing large numbers of defecations, and the intermediate position of *T. infestans* was observed. In Table 7 we have combined some of these characteristics in a "defecation index" (% of insects that defecated within 10 min $\times$ average number of defecations in 10 min/100) which allows us to make a rapid comparison of different stages of the same species and of different species.

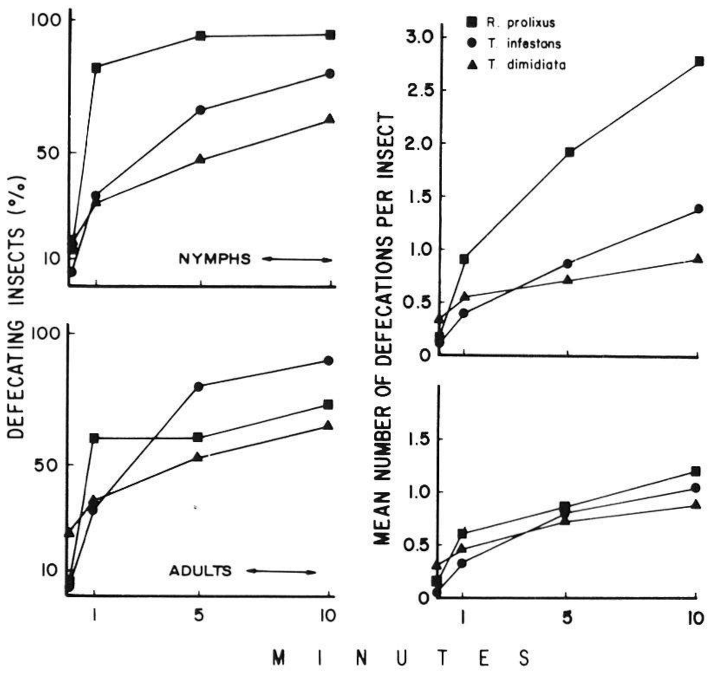

Fig. 2. Percentage of defecating insects and mean cumulative number of defecations per insect within 10 min in total nymphs and adults (30 individuals in each class).

Figs. 1 and 2 show the percentage of insects that defecated and the numbers of defecations within 10 min. During the first 60 sec, 70–90% of all *R. prolixus* instars had defecated, with the exception of the males, which did not reach 50%. The number of defecations per insect was higher in this species during the first 60 sec and generally continued to rise at a faster rhythm during the following minutes in the nymphs, the increment was slower in the adults, especially in the males. In *T. infestans* the number of defecating insects was below 50% during the first 60 sec but rapidly increased, with some differences between the instars, the first instar being markedly inferior; females were the most effective defecators. The number of defecations was low during the first 60 sec and rose slowly during the following minutes. In *T. dimidiata* the number of insects that defecated within the first 60 sec was similar to that of *T. infestans* due to the fact that some specimens defecated before completing the blood meal. Then the figures rose at a slower rate in all instars until the number defecating at 5 min barely reached 50%, with the exception of the females that surpassed this figure; data for males and first instar nymphs were much lower. Nymphs in the 5th instar defecated more frequently during feeding and therefore were more effective than the others; the females were less effective and the other instars even less, particularly first instars and males. In general, males in the three species tended to be the least effective regarding time of defecation, frequency of defecations and percentage of defecating insects, within a given time.

If we add the number of the nymphs and adults separately for each species and compare the percentage of insects that defecated during 10 min, we find that the pattern of the species is the same; that is, *R. prolixus*, especially the

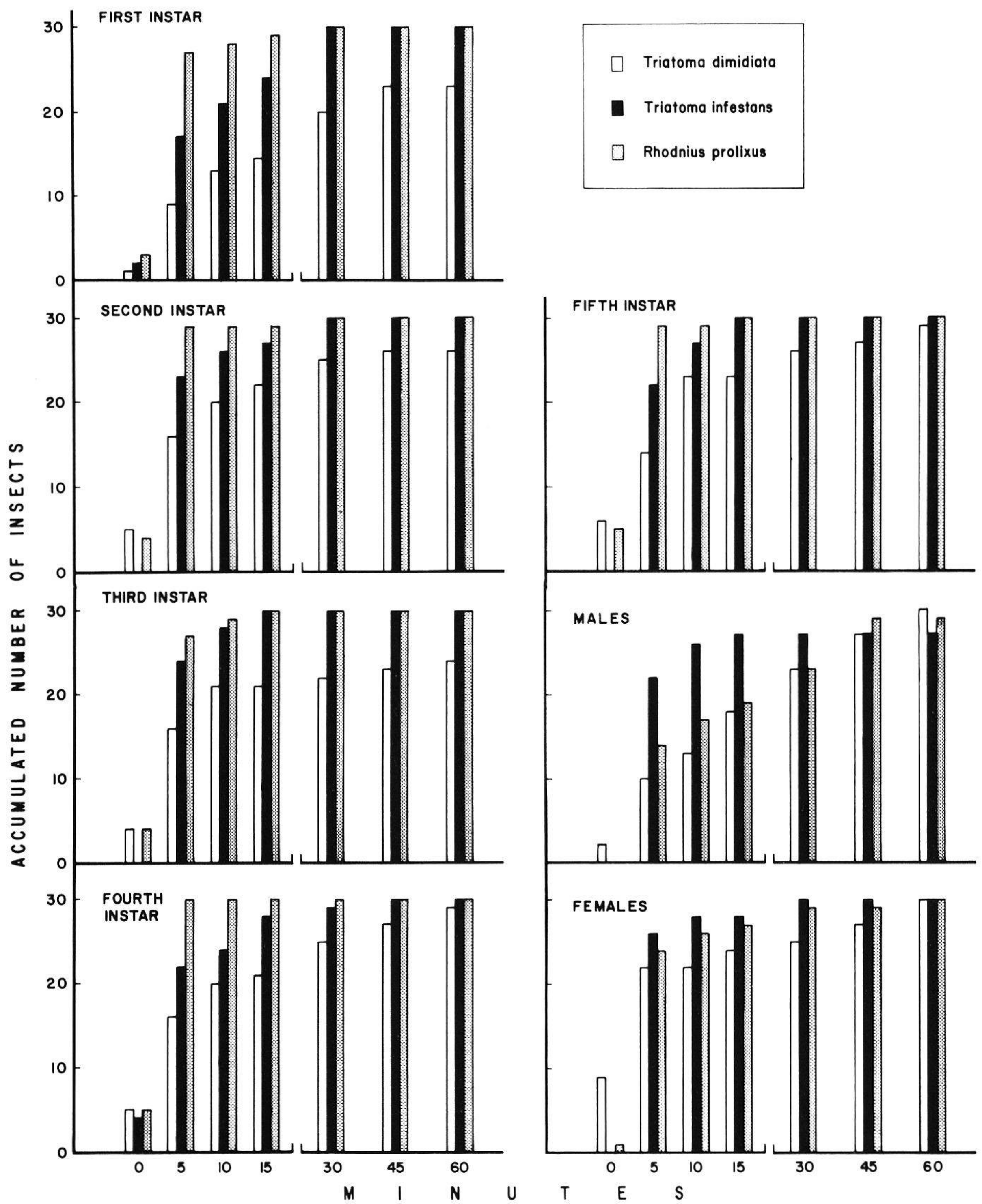

Fig. 3. Accumulated numbers of insects which defecated in one hour, by instar and sex (30 individuals in each class).

nymphs, was more efficient, followed by *T. infestans* and *T. dimidiata* (Fig. 2). The number of defecations followed a similar pattern; however, there was very little difference among adults of the three species and all were inferior to the nymphs. The nymphs of *R. prolixus* greatly surpassed those of the other two species. Figs. 3 and 4 show the differences up to one hour after feeding, by

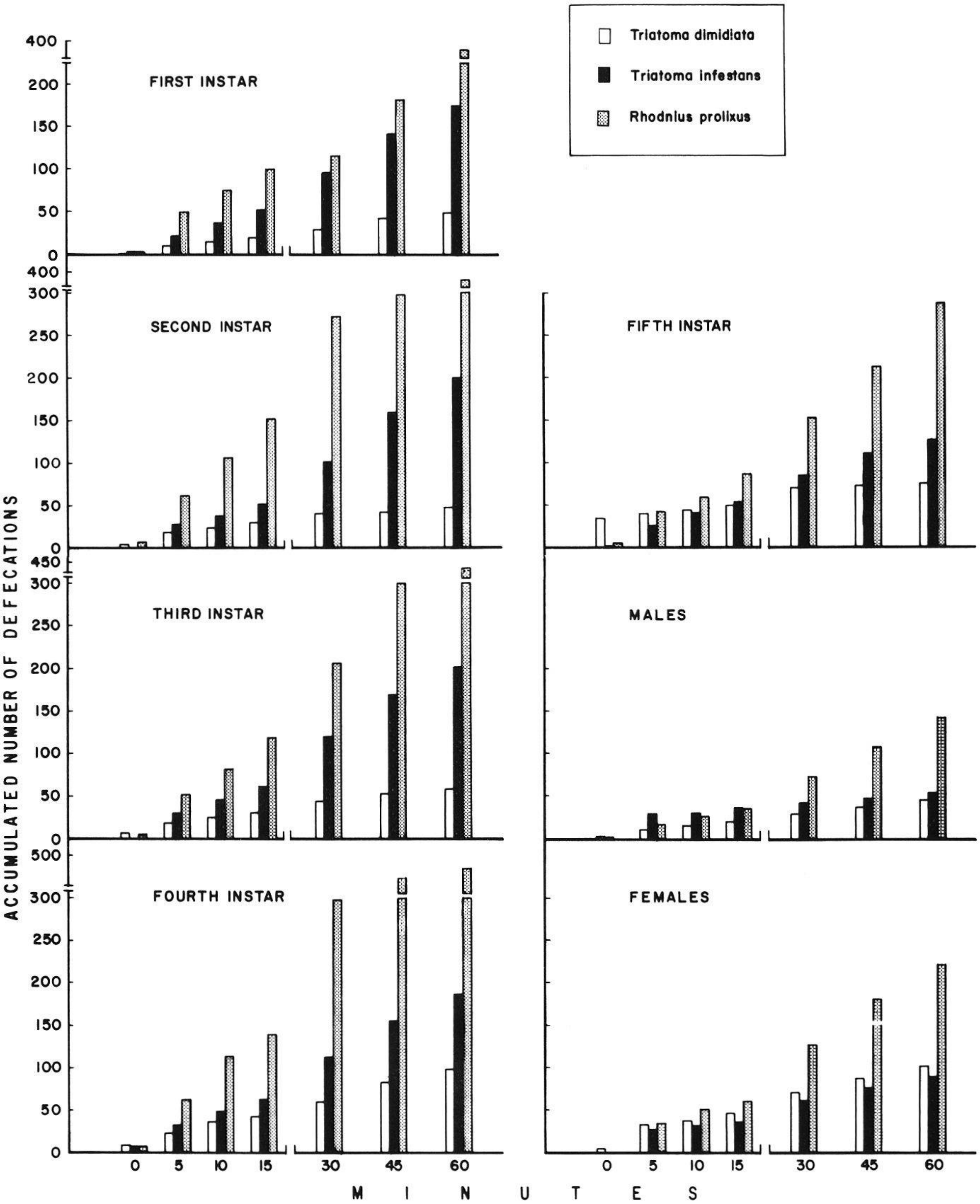

Fig. 4. Accumulated numbers of defecations in one hour, by instar and sex (30 individuals in each class).

instar, in the three species. In Fig. 3 it can be observed that practically all the *R. prolixus* and *T. infestans* defecated within the first 30 min, except the males. In Fig. 4 it is evident that *R. prolixus* amply surpassed the other two species in number of defecations throughout the period; however, the males were outperformed by *T. infestans* during the first 10 min. Defecations by female *T. dimidiata* exceeded those of *T. infestans* from the beginning.

Discussion

Comparisons of our data with those of other authors are difficult in view of the differences in experimental techniques and the use of small numbers of insects. The frequent interruptions during feeding observed in *R. prolixus* and *T. infestans* by Dias (1956) were not observed in our experiments; it is possible that there are variations in stock strains of the insects. Differences in environmental temperature might also affect the patterns (Wood, 1951).

An interesting fact is that the most timid species was *T. dimidiata* and that this behavior was more evident in first and second instar nymphs. Petana (1967), in Belize, pointed out the same characteristic for first instar nymphs of this species. Such behavior might affect the probability that these small nymphs will complete their life cycle (Zeledón et al., 1970).

As stated, our results show a marked tendency in *R. prolixus* to defecate sooner and more frequently after a blood meal, exhibited in a greater percentage of individuals in all stages except adult males. Previous observations (Dias, 1956; Pipkin, 1968; Pippin, 1970) also showed that males are slower defecators. The above behavior of *R. prolixus* together with its aggressiveness, and the abundance of this species in human dwellings could make it the most effective vector of Chagas' disease. However, while species such as *T. infestans* may be inferior in some of the above-mentioned parameters, they present compensatory mechanisms, such as their high population densities and extraordinary adaptability to varied climatic conditions and to the domiciliary biotope (Zeledón, 1974). All these factors effectively contribute to the high prevalence of trypanosome infection where these two species are dominant.

In the case of *T. dimidiata* we believe that, besides its lesser efficiency in several of the parameters measured, its relatively lower population densities also contribute toward a lower prevalence of trypanosomiasis where it is the only or the principal vector. However, within this species the fifth instar nymphs and the females could constitute effective vectors in view of their defecation patterns. Also, the greater timidity of the species results in a more prolonged relationship with its victim, which could facilitate infection.

In view of the fact that little is known about the relationship with humans under natural conditions, we have assumed arbitrarily that the insect is in intimate contact with its victim at least during the first 5–10 min after feeding, possibly to unburden itself by urination as the added weight would tend to slow down its mobility.

It seems certain that other insects of this same group are slower defecators. If we apply the defecation index proposed above to the data published by Wood (1951, 1960) for the North American *T. protracta,* we obtain figures of 0.01–0.25. Dias (1956) noted great defecation variation in several South American species within a 3-hour period. *R. prolixus* was faster than *T. infestans,* while other species such as *T. sordida* and *T. vitticeps* retained their feces longer.

Pipkin (1968) also found *R. prolixus* to be a faster defecator that the Panamanian vector *R. pallescens*; in 30 min 96% of the *R. prolixus* had defecated while only 27% of *R. pallescens* had done so. Pippin (1970) also compared *R. prolixus* with the North American species *T. sanguisuga* and *T. gerstaerckeri* and found the first markedly superior within the first 2 min after feeding.

Defecation patterns and house insect densities are probably the main factors that influence the incidence and prevalence of Chagas' disease in an area. Timidity on the part of an insect could affect transmission in two opposite ways, either by diminishing the number of attacks in the victims when the need for a blood meal is not urgent or by increasing the time of contact when a full meal is required. Under similar conditions of insect densities in a house, the defecation index suggests that *R. prolixus* will behave as a more efficient vector than *T. dimidiata,* and that *T. infestans* will be intermediate.

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