

Autogeny in Three Species of Triatominae: *Rhodnius prolixus*, *Triatoma rubrovaria*, and *Triatoma infestans* (Hemiptera: Reduviidae)

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ABSTRACT Autogeny, the capacity of a female to lay eggs without having ingested any blood meal in the adult stage, was studied in three species of Triatominae: *Triatoma infestans*, *Triatoma rubrovaria*, and *Rhodnius prolixus*. When nymphs of *T. rubrovaria* and *R. prolixus* were fed chicken blood, autogeny occurred frequently, even with only one meal. In *T. infestans* autogeny was frequent as well, but demanded at least two nymphal blood meals. Total number of autogenic eggs was positively correlated with the body weight of the adult female. We conclude, therefore, that autogeny is common in Triatominae.

KEY WORDS Insecta, autogeny, *Triatoma*, *Rhodnius*

AUTOGENY, the phenomenon whereby a female insect produces eggs without having ingested any proteinaceous food in the adult stage, has been described in several insect orders (Engelmann 1970). Although autogeny has been reported in several species of Triatominae, (e.g., *Rhodnius prolixus* Stål [Buxton 1930, Goodchild 1955], *Triatoma infestans* Klug [Perlowagora-Szumlewicz 1969], *Triatoma dimidiata* Latreille [Zeledon et al. 1970], *Triatoma brasiliensis* Neiva [Perondini et al. 1975], and *Triatoma pallidipennis* Stål [Noriega, 1987]), few quantitative studies exist on the phenomenon.

The presence of autogeny depends on genetic factors (O'Meara & Krasnisk 1970, Spielman 1975), as well as on the diet received by the insect during its preimaginal life (Perondini et al. 1975, Patterson 1979). In *R. prolixus* autogeny can even be abolished depending on the blood source utilized (Valle et al. 1987).

Here, we describe the results of a quantitative study of autogeny in three species of Triatominae fed on chicken blood during their preimaginal life. The following were analyzed: the effect on autogeny of the number of meals taken during the fifth-larval instar; the effect of mating; and oviposition features such as preoviposition period, oviposition period, and number of eggs laid.

Materials and Methods

Insects were fed once a week directly on restrained chickens, and maintained at 30°C, 50-

70% RH, and a 12:12 (L:D) photoperiod (Noriega 1987).

Females were weighed immediately after the imaginal molt and isolated in individual tubes together with two recently fed males. The mating was checked by observation of the spermatophore. The number of eggs laid by each female was monitored daily until the end of oviposition (minimum 30 d).

Analyses of variance tested significance of differences in number of eggs laid, duration of preoviposition and oviposition periods, and number of eggs laid per day per female (Wilkinson 1986). Differences between percentages of hatched eggs and molting insects were analyzed with the test of equality between percentages (Sokal & Rohlf 1969). Chi-square analysis tested differences in the frequencies of autogenic females when different number of meals were taken by fifth-instar nymphs and to test differences in the number of eggs laid by mated and virgin females. Regression analyses examined relationships between female weight, duration of preoviposition and oviposition periods, and the number of eggs laid per day per female as functions of the total number of eggs laid by a female (Sokal & Rohlf 1969).

Results

The percentages of insects that molt after receiving a single blood meal in the fifth instar were 25.7% ($n = 544$) for *T. infestans*, 47.7% ($n = 107$) for *T. rubrovaria*, and 100% ($n = 167$) for *R. prolixus*. Differences among species were significant ($P \leq 0.05$). The weight of newly emerged adults increased with the amount of blood in-

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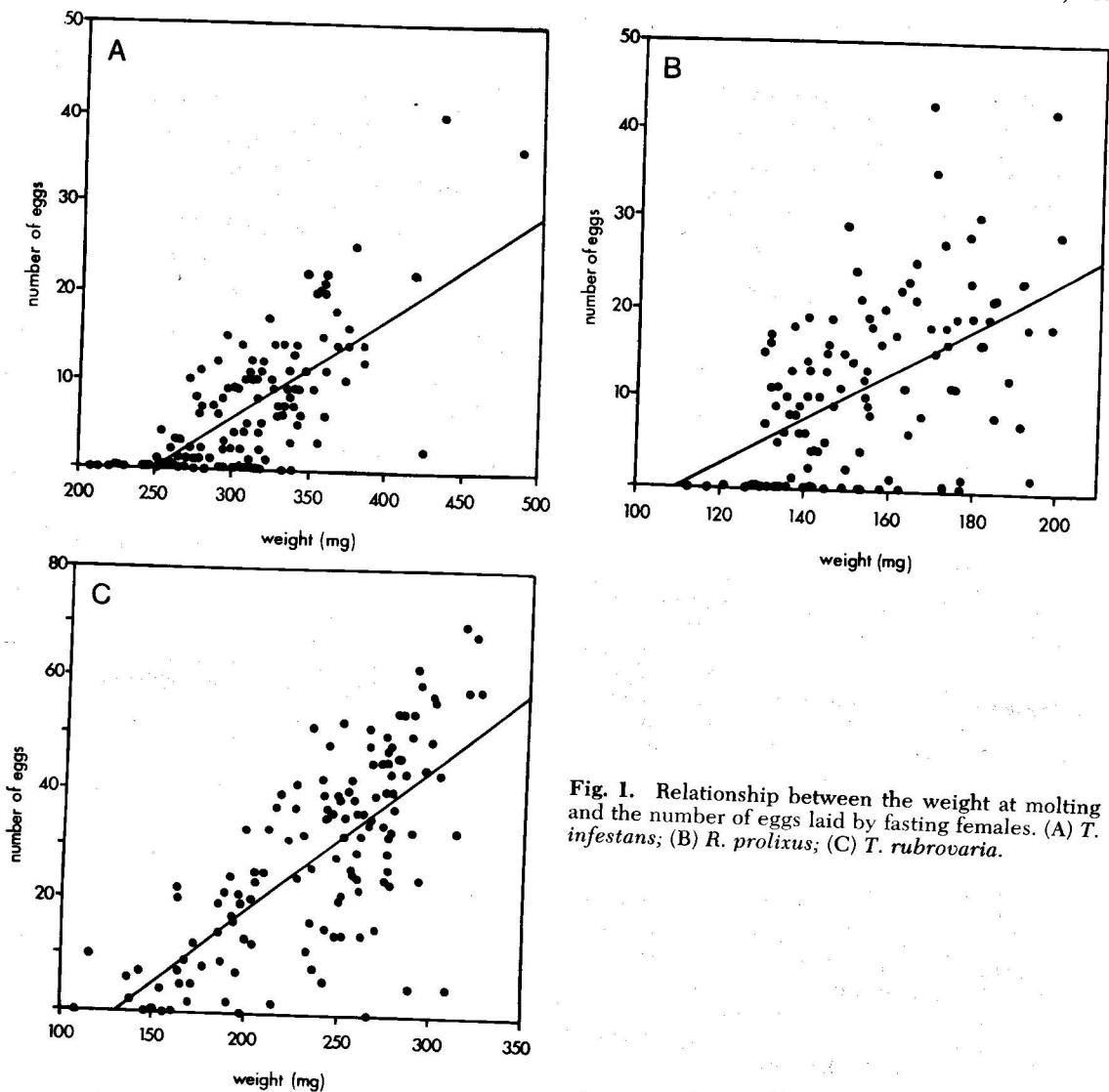


Fig. 1. Relationship between the weight at molting and the number of eggs laid by fasting females. (A) *T. infestans*; (B) *R. prolixus*; (C) *T. rubrovaria*.

gested by fifth-instar larvae (Noriega 1987). Adult females had to reach a minimum weight to lay autogenic eggs. The minimum weight for all three species (114, 134, and 250 mg for *R. prolixus*, *T. rubrovaria*, and *T. infestans*, respectively [Fig. 1]) was lower than the average weight of females randomly taken from the colony (Table 1). A strong correlation was observed between the female weight and the number of eggs laid (Table 2). The percentage of autogenic females increased with the number of meals received during the fifth instar (Fig. 2). When the frequencies of autogenic versus nonautogenic females taking one meal or more than one meal were compared by chi-square, there was a significant difference in all species (*T. rubrovaria*, $\chi^2 = 14.8$; *R. prolixus*, $\chi^2 = 4.7$; *T. infestans*, $\chi^2 = 77.3$; all $df = 1$, all $P \leq 0.05$). The average number of autogenic eggs laid varied between 9 and

30 in the different species, and the maximum number of eggs ranged from 40 to 70 (Table 1). The preoviposition period of fasting females varied between 7 and 10 d, depending on the species (Table 1). The number of eggs laid per day per female, the total oviposition period, and the percentage of hatched eggs are presented in Table 1. The relation between these different parameters was analyzed and the regression coefficients, presented in Table 2, indicate that for each species the larger females showed a shorter preoviposition period, a higher rate of eggs laid per day, a longer oviposition period, and therefore a higher total number of eggs laid (Table 2). The mortality during the first 30 d after emergence was low for the three species: 1.6% (*R. prolixus*), 5.0% (*T. rubrovaria*), and 7.0% (*T. infestans*). With *T. rubrovaria* and *T. infestans* significant decreases were found in the number of

Table 1. Parameters of autogeny

Parameters	<i>T. rubrovaria</i>	<i>R. prolixus</i>	<i>T. infestans</i>
\bar{x} Weight of female at moulting (mg)	236.6 \pm 49.2 (n = 135)	154.1 \pm 20.3 (n = 117)	305.6 \pm 46.2 (n = 151)
\bar{x} no. eggs laid by a female \pm SEM	29.9 \pm 16.3 ^a (n = 126)	14.5 \pm 8.5 ^a (n = 90)	9.1 \pm 7.0 ^a (n = 105)
Max no. eggs laid by a female	70	43	40
No. eggs/day/female \pm SEM	2.3 \pm 0.9 (n = 84)	2.7 \pm 1.0 (n = 57)	2.4 \pm 0.8 (n = 28)
Preoviposition period (d) \pm SEM	7.5 \pm 1.8 ^a (n = 86)	7.7 \pm 1.1 ^b (n = 57)	10.7 \pm 2.3 ^{a,b} (n = 30)
Oviposition period (d) \pm SEM	15.1 \pm 4.4 ^a (n = 85)	6.2 \pm 2.8 ^a (n = 57)	3.4 \pm 0.4 ^a (n = 28)
% Hatched eggs	88.8 ^a (n = 1,404)	62.5 ^{a,b} (n = 336)	88.8 ^b (n = 36)

^{a,b} Significantly different ($P < 0.05$).

eggs laid by virgin fasting females when compared with mated fasting females of the same weight; virgin *T. rubrovaria* females laid 49.8% of the number of eggs laid by mated females (mated: $\bar{x} = 27.3 \pm 13.1$, $n = 20$; virgin: $\bar{x} = 13.6 \pm 7.2$, $n = 34$) ($P \leq 0.05$); virgin *T. infestans* did not lay eggs (mated: $\bar{x} = 7.4 \pm 6.9$, $n = 40$; virgin: $\bar{x} = 0$, $n = 4$) ($P \leq 0.05$). Virgin *R. prolixus* females laid only 15% of the number of eggs laid by mated females (mated: $\bar{x} = 8.8 \pm 9.8$, $n = 45$; virgin: $\bar{x} = 1.3 \pm 1.8$, $n = 7$); in this case the differences were very close to be significant ($P = 0.051$).

Discussion

The use of identical experimental conditions (diet and rearing conditions) allowed us to perform a comparative analysis of the effect of larval nutrition on autogeny in three species of Triatominae. Larval nutrition is known to play an important role in the control of egg production and autogeny in many insect species (Engelmann 1970). The effect of larval nutrition on egg production was described in *R. prolixus* (Patter-

son 1979, Valle et al. 1987) and *T. brasiliensis* (Perondini et al. 1975). The number of eggs laid by fasting *R. prolixus* females is correlated with the amount of blood remaining in the stomach from the last larval meal (Davey 1989); however, not only the amount of food ingested during the larval stage, but also the source of the blood appears to be very important. Fifth instar larvae of *R. prolixus*, when fed on sheep blood, do not show autogeny; however, autogeny does occur when the same insect is fed on human (Valle et al. 1987) or rabbit blood (Davey & Singleton 1989). Autogeny was not detected in *T. infestans* when fed on guinea pigs (Regis 1979). In contrast, we found that *T. infestans* does show autogeny when fed on chicken blood. Therefore, a specific blood source can have different effects depending on the insect species used, although it can not be excluded that different strains or populations show different behaviour. Under our experimental conditions, using chicken blood as the food source, the three species studied all developed autogenic eggs, which allowed a comparative analysis of autogeny in these species.

Table 2. Parameters of regression between the number of eggs laid by a female and the weight of emerged female, the duration of preoviposition and oviposition period, and the number of eggs laid per day by a female

Dependent-independent variables in regression	n	Intercept	Slope	r ²
<i>T. rubrovaria</i>				
No. eggs-weight female	126	-31.09	0.252	0.494**
No. eggs-preoviposition period	86	9.82	-0.067	0.328**
No. eggs-eggs/day	84	0.54	0.051	0.674**
No. eggs-oviposition period	85	9.92	0.147	0.282**
<i>R. prolixus</i>				
No. eggs-weight female	90	-15.60	0.190	0.184**
No. eggs-preoviposition period	57	9.02	-0.079	0.251**
No. eggs-eggs/day	57	1.22	0.097	0.307**
No. eggs-oviposition period	57	3.28	0.186	0.230**
<i>T. infestans</i>				
No. eggs-weight female	104	-29.03	0.119	0.469**
No. eggs-preoviposition period	30	11.57	-0.099	0.155*
No. eggs-eggs/day	28	1.77	0.085	0.314*
No. eggs-oviposition period	28	1.57	0.215	0.561**

* $P < 0.05$. ** $P < 0.01$.

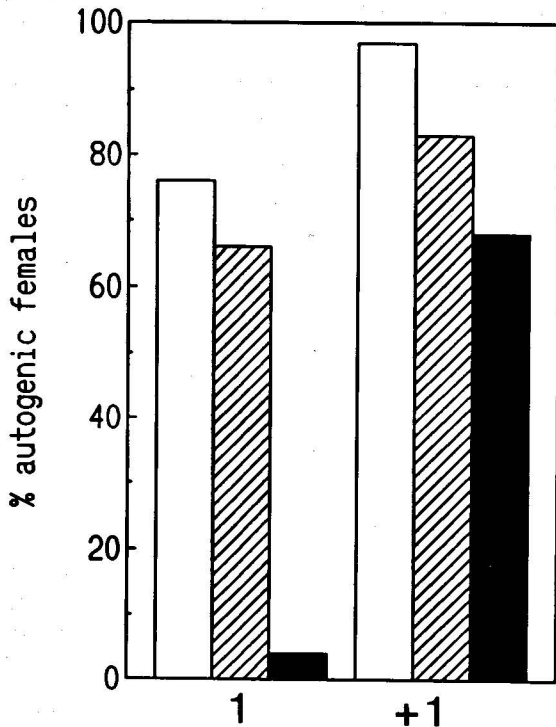


Fig. 2. Percentage of autogenic females obtained with different numbers of meals during the fifth instar. 1, one meal; +1, more than one meal. Open bars, *T. rubrovaria* (1: $n = 25$; +1: $n = 110$); cross-hatched bars, *R. prolixus* (1: $n = 52$; +1: $n = 69$); filled bars, *T. infestans* (1: $n = 70$; +1: $n = 147$). All differences between insects from the same species as $P \leq 0.05$, see text for χ^2 analysis.

Percentages of autogenic females and averages of eggs laid varied among species. Under the conditions described here, autogeny appeared a common phenomenon in *T. rubrovaria* and *R. prolixus*, even after one nymphal blood meal (Fig. 2). Of *R. prolixus* fifth instar nymphs, 100% molted with only one meal, and 66% of these adults laid autogenic eggs; in contrast, although only 50% of *T. rubrovaria* fifth instar nymphs molted after one meal, 76% of these adults were able to lay autogenic eggs (Fig. 2). *T. infestans* fifth-instar nymphs demanded at least two meals to molt and lay autogenic eggs. Only 26% of fifth-instar nymphs molted after a single blood meal, and 4% of these females were autogenic. For all three species there was a significant increase in the frequency of autogenic females when fifth instar nymphs were fed more than once ($P \leq 0.05$). Animals fed to repletion as larvae are not only large in size following ecdysis to the adult, they also possess large fat bodies (Patterson 1979), and their crop contains a larger amount of undigested blood (Patterson 1979, Montenegro 1983). These reserves allow fasted adults to lay autogenic eggs (Davey & Singleton 1989).

When adults fasted, the total number of eggs laid was positively correlated to the weight of the adults (Fig. 1). As a general observation, we found that, within each species, the females that stored more reserves during their preimaginal life enhanced their reproductive capacity and laid more eggs (Table 2). In addition, the insects showed a shorter preoviposition period, a higher rate of eggs laid per day, and a longer oviposition period (Table 2). *T. rubrovaria* and *R. prolixus* showed similar rates of eggs laid per day and per female, but *T. rubrovaria* had a longer period of oviposition (Table 1). This allowed the latter species to lay the double amount of eggs compared with *R. prolixus*. This fact could be related to a higher capacity of nymphs to store reserves.

Autogeny did not have any effect on the viability of females and eggs: the mortality of the autogenic females and the percentage of hatched eggs did not differ from those usually found in nonautogenic females in our laboratory (Noriega 1987).

The influence of mating upon oocyte maturation and oviposition varies between species (Engelmann 1970). In *R. prolixus* mating affects the digestion (Wigglesworth 1948), enhances egg production, and increases the rate of oviposition (Pratt & Davey 1972, Davey 1987). Virgin females of *R. prolixus* (Buxton 1930, Pratt & Davey 1972) and *T. brasiliensis* (Brasileiro 1982) mature and oviposit some eggs, but both processes are increased when mating occurs. We found a significant decrease in the number of eggs laid by virgin fasting females of *T. rubrovaria* and *T. infestans*. Davey & Singleton (1989) did not find statistically significant differences in egg production between mated and virgin females of *R. prolixus*, that were fed on rabbit; however, in our study the differences in *R. prolixus* were close to being significant; differences in the sizes of the samples, as well as in the source of blood (chicken versus rabbit), could account for the variation.

The results of these experiments, and the fact that autogeny was also observed in *T. pallidipennis*, *T. guasayana* Wygodzinsky and Abalos, *T. vitticeps* Stål, *Panstrongylus megistus* Burmeister (Noriega 1987), *T. brasiliensis* (Perondini et al. 1975), and *T. dimidiata* (Zeledon et al. 1970) allow us to conclude that autogeny is common in Triatominae.

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