

A population-dynamics simulation model of the main vectors of Chagas' Disease transmission, *Rhodnius prolixus* and *Triatoma infestans*

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ABSTRACT

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A simulation model was developed to represent the population dynamics of two bugs (*Triatoma infestans* and *Rhodnius prolixus*), which are the main vector species of Chagas' Disease in some Latin American countries. The model includes the infection process of bugs with the parasite causing the disease (*Trypanosoma cruzi*). Human and animal hosts for bugs (with a preference factor for each) were considered; bug migration between houses and between houses and the wild environment was also modelled; the three types of houses most common in rural areas were considered. The bugs' population regulation mechanisms were modelled acting over natality and mortality. The population parameters of the two bug species that had no independent actual estimation were calibrated with a field series available only for *R. prolixus*.

Populations of both species showed sustained oscillations under certain conditions, with about two cycles per year for *T. infestans* and about four cycles per year for *R. prolixus*, and proportional to the length of each species' development time. Development-stage class distribution alternations are associated with these oscillations; adults are most abundant when population size is at its minimum. The symmetry of the fluctuation seems to be affected by female fecundity. Sensitivity analyses show that the main parameters affecting the stability behavior of the vector populations were: (a) the threshold nymphal density at which irritation of the host starts, (b) female fecundity, (c) number of hosts available, and (d) the emigration rate. The threshold nymphal density at which irritation of the host starts, combined with female fecundity, proved critical in producing a change in the stability behavior of the population, from a stable point equilibrium to a limit cycle. These results, if incorporated into transmission control models, can be used to optimize control strategies.

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INTRODUCTION

Chagas' Disease is one of the most serious current health problems in Latin America, affecting about 16 to 18 million people, of whom approximately 2.5 million are found in Argentina (Moncayo-Medina, 1987). Difficulties in its control arise from the ecological characteristics of the insect vectors and the complex socioeconomic aspects of the human population at risk. The parasite causing this disease (*Trypanosoma cruzi*) is transmitted by two main vector species, *Triatoma infestans* and *Rhodnius prolixus* (Reduviidae: Triatominae).

There are several mathematical models of the population dynamics of these two vector species: life-table models were applied to *T. infestans* (Rabinovich, 1971; Rabinovich and Dorta, 1973; Rodriguez, 1977), and a life-cycle model was developed for *R. prolixus* (Soriano and Luis, 1977) as well as a logistic model (Rabinovich and Rossell, 1976; Rabinovich, 1985). These models are strong in dynamic relationships and parameter estimation, but poorly reflect the actual environmental conditions of epidemiological importance, such as the number of bug hosts and their type (human or animal), and the type of dwelling the people inhabit.

We present here the results of a Chagas' Disease vector population-dynamics simulation model that deals with the above weaknesses by incorporating the following features: (a) hosts differentiated as animal and human, with insects showing a certain preference for each; (b) density-dependent vector population regulation acting independently through bug mortality and natality; (c) different kinds of houses; and (d) migration of bugs occurring to and from houses, and to and from wild refuges. The model was used to analyze the stability behavior of the vector population, and to discuss its relevance to the epidemiology of the disease. For the latter purpose the dynamics of the infection in the vectors had to be modelled. This is the first case of a mathematical model of Chagas' Disease transmission where calibration was performed with a set of data available for *R. prolixus*.

DESCRIPTION OF THE MODEL

The spatial unit was the human dwelling, the time unit was one day and the time horizon 20 years. The species modelled were *R. prolixus* and *T. infestans*, and their population dynamics were simulated separately. Figure 1 shows the basic processes and components considered in this model. The basic assumptions for developing the model are given in Table 1. Figure 2 shows the relationships between variables and factors of the three main processes modelled: natality, mortality and migration; their mathematical

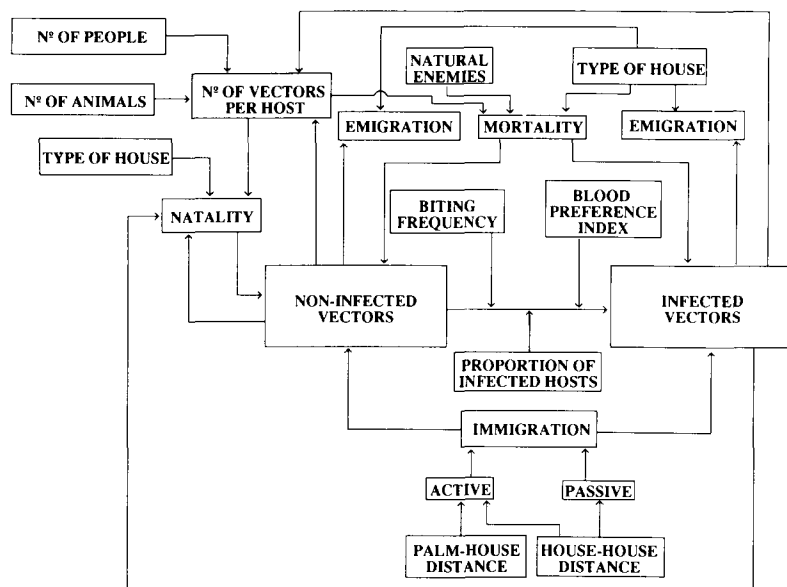


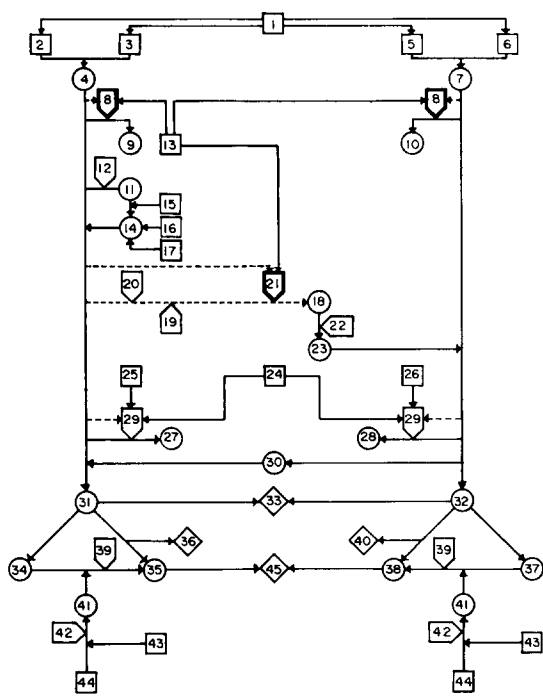
Fig. 1. Block diagram of the basic components and processes of the population-dynamics model of two Chagas' Disease vectors: *R. prolixus* and *T. infestans*. It is applicable to each species separately, with the only difference that palm-house immigration does not occur in *T. infestans*.

relationships are shown in Table 2. The hosts were differentiated as human and animal populations, with stable numbers of 10 and 17, respectively (the latter constituted by 14 chickens and three dogs from old houses with *R. prolixus* (Rabinovich et al., 1980) and nine people and three dogs for houses with *T. infestans* (Wisnivesky, personal communication, 1988). A biting-preference index for blood from these hosts was used (Wisnivesky-Colli, 1987): 90% and 30% preference for humans for *R. prolixus* and *T. infestans*, respectively, where the index expresses percent of meals on humans with respect to total meals (human and animal).

Three kinds of houses were considered: (a) type 1, a typical shack of mud walls and palm or branch roof; (b) type 2, a house with mud walls and tin roof; and (c) type 3, a dwelling built of bricks and cement. As the bugs hide in the roof and wall cracks, the number of refuges available decreases from type 1 to 3. The vector carrying-capacity of each type of house (Table 2) is related to the amount and kind of refuges available.

The vector's population-density regulation mechanism is a food-limited process but responds to accessibility of the hosts and not to their numbers (Schofield, 1980a, b, 1982; Weir-López, 1982; Rossell, 1984). The higher the number of insect bites per person per night, the higher the irritation

produced to the human and animal host. Due to this irritation, and the victims' response to it, the bug's blood ingestion is interrupted, producing: (a) a reduction in fecundity (fewer eggs per female per day); (b) an increase in mortality due to higher predation by natural enemies (chickens, lizards,



- variables (numbers that change during the simulation)
- parameters (constant numbers or initial value of a variable)
- ⬠ constant coefficients (constant rates or proportions)
- ⬡ variable coefficients (variable rates or proportions)
- ◇ output (variables used as results for statistics)
- flux (a variable changes by the influence of another variable, with the latter being modified after the change)
- > effect (a variable changes by the influence of another variable, with the latter remaining unaffected)

spiders), associated with a higher number of feeding attempts; and (c) an increase in mortality due to starvation. These three mechanisms are represented algebraically in Table 2. Mechanisms (a) and (c) depend upon a threshold value: the number of insects per person per night that triggers an irritative response; this value was initially considered to be 100 bites per person per night. However, it was assumed that the effect of reduced feeding due to irritation of the host would be felt more rapidly for (a) than for (c); thus, the threshold was kept at 50 bites per person per night for the effect upon fecundity. The form of the function was the same for (a) and (c): a straight line with the same intercept with the x -axis.

The starvation function (mechanism b) has an 'S' shape with two critical values: the base mortality and a very steep vertical branch. The base line had a different value for nymphs and adults, and also differed for *R. prolixus* and *T. infestans*, and the slope was calibrated to regulate the

Fig. 2. Diagram of variable and parameter relationships, for one unit day of simulation, of the Chagas' Disease vector population-dynamics simulation model. Names in capital letters and between parentheses are variables, parameters and coefficients from Table 2. Interpretation of figures: 1, Total number of bugs at day 1 of simulation; 2, Total number of non-infected adult bugs at day 1 of simulation; 3, Total number of infected adult bugs at day 1 of simulation; 4, Total number of adults at day 1 of simulation; 5, Total number of non-infected nymphs at day 1 of simulation; 6, Total number of infected nymphs at day 1 of simulation; 7, Total number of nymphs at day 1 of simulation; 8, Starvation density-dependent mortality coefficient (TMN and TMA for nymphs and adults, respectively); 9, Total number of dead adults from starvation; 10, Total number of dead nymphs from starvation; 11, Total number of emigrating adults (NE); 12, Emigration coefficient (TE); 13, Total number of hosts; 14, Total number of immigrating adults (NI); 15, Fraction of emigrating adults that will immigrate to other houses (FR); 16, Number of passive immigrating adults (associated to social visiting rate, see Table 2); 17, Number of active immigrating adults (associated with palm emigration rate, see Table 2); 18, Oviposition (number of eggs laid) (NH); 19, Natality coefficient (TNATCH); 20, Female proportion (PH); 21, Density-dependent factor affecting natality (FN); 22, Hatching coefficient (EM); 23, Number of nymphs emerging from hatched eggs (NNE); 24, Carrying capacity (K_j); 25, Basic adult mortality (MB_a); 26, Basic nymph mortality (MB_n); 27, Total number of dead adults by predators and natural mortality; 28, Total number of dead nymphs by predators and natural mortality; 29, Predator and natural mortality coefficient (MNN and MNA for nymphs and adults, respectively); 30, Number of nymphs moulting to adults; 31, Total number of adults at day 2 of simulation; 32, Total number of nymphs at day 2 of simulation; 33, Total number of bugs at day 2 of simulation; 34, Total number of non-infected adults at day 2 of simulation; 35, Total number of infected adults at day 2 of simulation; 36, Fraction of infected adults; 37, Total number of non-infected nymphs at day 2 of simulation; 38, Total number of infected nymphs at day 2 of simulation; 39, Daily biting rate (FP); 40, Fraction of infected nymphs; 41, Total number of infected hosts (PAR); 42, Parasitaemic proportion of chronic human hosts; 43, Number of parasitaemic animal hosts; 44, Number of parasitaemic human hosts; 45, Total number of infected bugs.

TABLE 1

Implicit and explicit assumptions and simplifications used in the Chagas' Disease vector population-dynamics simulation model, in addition to the algebraic ones presented in Table 2

Explicit

- (1) The bug population is composed of eggs, an immature stage (nymphs of any of the five instars), and adults
- (2) The developmental times of eggs and of the immature stage are considered constant
- (3) Adult bugs have a pre-reproductive time of 10 days for both species
- (4) The sex-ratio of the adult bug population is 50:50
- (5) Only adult bugs migrate
- (6) All non-human hosts have a constant population growth-rate of 10% per year
- (7) The host populations are considered to remain constant after reaching ten, 14 and three people, chickens, and mammals per house, respectively
- (8) The bugs feed selectively upon animals and humans; the preference index for humans is 90% and 30% for *R. prolixus* and *T. infestans*, respectively; for definition of the index see text.

Implicit

- (1) Climatic effects and seasonality are not considered
 - (2) There are no individual differences between insects of the same kind
 - (3) The *T. cruzi* parasite has no effect upon mortality, reproduction and migration of the insect vector.
 - (4) Probability of infection of bugs is the same for nymphs and adults
 - (5) The density-dependent functions that involve the irritation of the vertebrate hosts are the same for any kind of host
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population at the average carrying capacity determined by the type of house (2100, 700, and 120 for *R. prolixus* for house types 1, 2, and 3, respectively; 900, 350, and 100 for *T. infestans* for house types 1, 2, and 3, respectively). The values of the carrying-capacity-related constants that keep average populations at those levels are shown in Table 2.

Field data (Rabinovich et al., 1980) showed that both emigration and immigration were density-independent, and that emigration occurred at a daily constant rate given as a fixed proportion of the adult population size (Table 2). Immigration has two sources; passive and active; the former takes place when the insects are carried by people, and the latter occurs when adult insects disperse by flight; this active immigration can originate from other houses of the same village, or from wild environments (mainly palms in tropical areas).

When density-dependent regulation parameters (FN1, FN2, FS1, FS2, FS3, TE1, TM1, TM2 and TNATCH) had no field or experimental estimates available, a numerical calibration experiment was performed that produced parameter

TABLE 2
Vector's functions and algorithms used in the model (all rates are in day units, except when indicated)

Process	Function	Parameter or variable	Unit	Value for <i>R. prolixus</i>	Value for <i>T. infestans</i>	Source
Development time	DT = EDT + NDT	DT	Time from egg laid to mature female	days	170	Rabinovich (1972), Rodriguez (1977)
		EDT	Time from egg laid to egg hatched	days	20	Rabinovich (1972), Rodriguez (1977)
		NDT	Time from egg hatched to mature female	days	150	Rabinovich (1972), Rodriguez (1977)
Fecundity	NH = TNATCH * FN	FN	Natality factor	–	variable	–
	* VA * PH	FN1	Threshold density at which irritability starts	bugs/host	50	calibration
	FN = [FN2 – (D/AL)]					
	/ (FN2 – FN1)	FN2	Density at which reproduction stops	bugs/host	1000	calibration
		D	Density	bugs/house	variable	–
Hatching		AL	Food sources	No. of hosts	variable	–
		NH	No. of eggs laid	eggs	variable	–
		TNATCH	Natality rate	eggs/female	0.77	Rabinovich (1972)
		VA	Adult population	bugs/house	variable	–
		PH	Sex ratio (♀/adults)	–	0.5	Rabinovich (1981)
	NNE = NH	NNE	Number eggs producing nymphs	eggs/house	variable	–
	* (1 – EM) ^{EDT}	EM	Daily egg mortality coefficient	–	0.008	Rabinovich (1972), Rodriguez (1977)
				0.003		

To be continued...

TABLE 2 (continued)

Process	Function	Parameter or variable	Unit	Value for <i>R. prolixus</i>	Value for <i>T. infestans</i>	Source
Natural mortality (includes predation)	$MNA = MB_a + (1 - MB_a) / [1 + (K_j/D)^{20}]$	MNA MB _a Adult mortality rate Basic adult mortality rate	- -	variable 0.007	variable 0.001	- Rabinovich, (unpublished)
	$MNN = MB_n + (1 + MB_n) / [1 + (K_j/D)^{20}]$	MNN Nymph mortality rate	-	variable	variable	-
	MB _n	Basic nymph mortality rate	-	0.009	0.005	Rabinovich (u), Rabinovich (1972)
	K _j	Carrying capacity-related constant	bugs/host	3000 _{j=1} 600 _{j=2} 150 _{j=3} 1, 2, 3 variable	1300 _{j=1} 500 _{j=2} 150 _{j=3} 1, 2, 3 variable	Rabinovich (unpublished)
	j	House type	-	-	-	-
Starvation mortality	$TMA = [FS2 - (D/AL)] / (FS2 - FS1)$	TMA Adult starvation mortality rate	-	-	-	-
	FS1	Threshold density at which irritation starts	bugs/host	200	200	calibration
	FS2	Density at which there is no survival	bugs/host	1000	1000	calibration
	TMN	Nymph starvation mortality rate	-	variable	variable	-
	FS3	Same as FS1 but for nymphs	bugs/host	100	100	calibration

Migration	NI = (D * TE * FR) + (FV _i * PC / 360) + IP	NI	Immigrating adults	adults/house	variable	—
		TE	House emigration rate	—	0.15	Rabinovich et al. (1980)
	NE = D * TE	FR	Fraction of emigrants that return	—	0.25	Rabinovich (1981)
		FV _i	No. of bugs per visit	—	1 _{i=1} 0.5 _{i=2} 0 _{i=3}	Rabinovich (1981)
		PC	Social visiting rate	visits/year	6	Rabinovich (1981)
		IP	Palm emigration rate	bugs/day	1	Rabinovich (1981)
	PI = PP * PAR * FP /AL	i	Community type	—	1, 2, 3	scenario
		NE	Emigrating adult	adults/house	variable	—
		PI	Proportion of bugs that become infected	—	variable	—
		PP	Bug infection probability after biting an infected host	—	0.5	Schenone et al. (1977)
Vector infection	PAR	PAR	Infected hosts	hosts/house	variable	—
		FP	Biting rate	bites/night	0.1	Rabinovich et al. (1979)

values satisfying the best fit between simulated results and an observed population-density time-series for *R. prolixus* (Rabinovich et al., 1980).

The behavior of the vector population size with time as a function of several variables and parameters was examined through a program designed to perform a sensitivity analysis. Four variables and parameters were selected as the ones that had an apparent sensitive effect on the population dynamics, because they appear in a multiplicative or exponential form in the dynamic equations of the model: the mortality density-dependent parameter (FS3), the two basic mortality rates (TM1 and TM2), and the fecundity rate (TNATCH). For the sensitivity analyses, three values were assigned to each parameter: the standard one given in Table 2, plus values 50% above and below it; the parameter changes were applied in all possible combinations simultaneously ($3^4 = 81$ combinations). Two indicators of sensitivity were used as output of 30-year simulations for each combination: the vector average stable population and its standard deviation. They were calculated by averaging the daily total population of vectors per year, and then computing the mean of means, and its standard deviation, for the *last* ten years of simulation. Only eggs were not included as part of the total population averages. The results of the 81 runs were subjected to a stepwise regression analysis, with the model parameters as independent variables and the two indicators of sensitivity as dependent variables. The standardized partial coefficients of regression were used to determine the relative importance of each independent variable in terms of the explanation of the variance of the dependent variables.

The model was developed in a MICROVAX II system, and the complete model took about 1 min to run for a 30-year simulation in one house.

RESULTS

Effects of the initial conditions upon the final stable results proved to be unimportant; as a consequence, simulations were performed using the following arbitrary initial conditions: 5 eggs, 65 nymphs and 5 adults for *R. prolixus*, and 80 eggs, 60 nymphs and 25 adults for *T. infestans*.

The calibration simulation provided the values of the density-dependent parameters FN1, FN2, FS1, FS2, and FS3 for *R. prolixus* (Fig. 3), and are given in Table 2. As there was no field information for *T. infestans*, the same values were assigned to this species.

The effects of different house types for 10 years of simulation are shown in Fig. 4 for *T. infestans* and *R. prolixus*; the bug populations fluctuate at the average levels of the carrying capacities of each house type. Both species display sustained oscillations; *T. infestans* shows about two cycles per year,

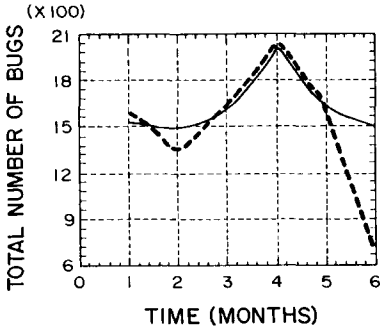


Fig. 3. Simulated (broken line) and field (solid line) populations of *Rhodnius prolixus*.

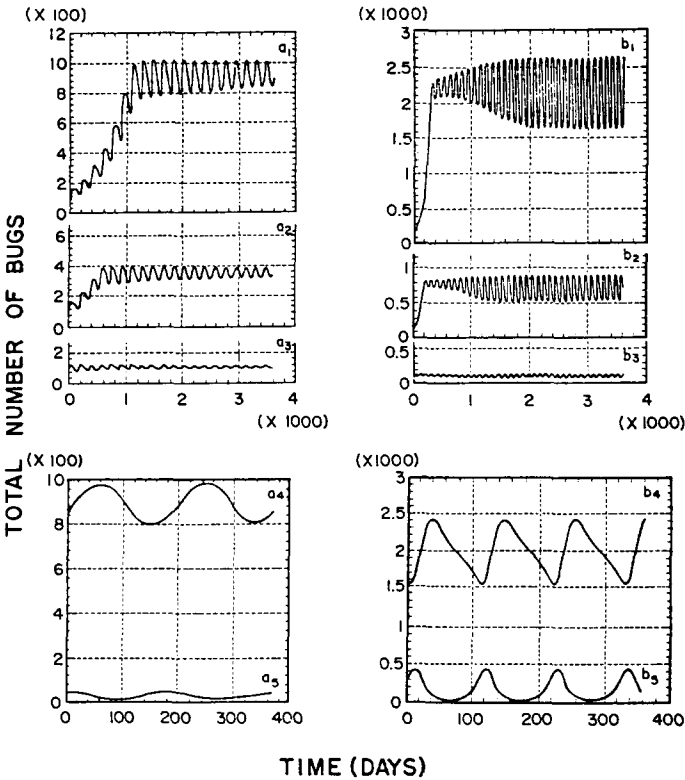


Fig. 4. Population oscillations of simulated *Triatoma infestans* (a) and *Rhodnius prolixus* (b) populations. Subindices 1, 2, and 3 correspond to house types 1, 2, and 3, respectively; subindices 4 and 5 correspond to nymphal and adult populations, respectively, after day 3000 (that is, after reaching stable oscillations) for house type 1.

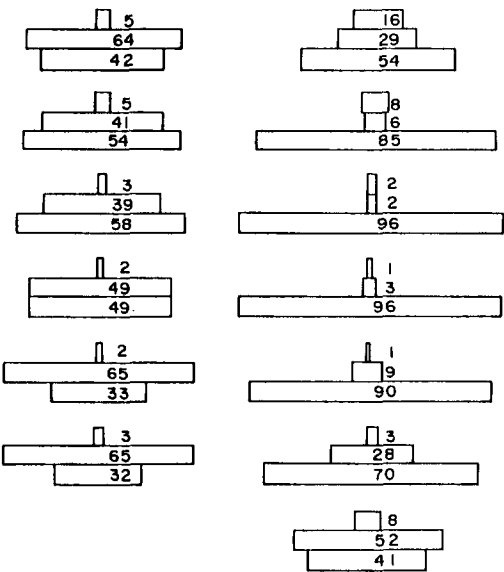


Fig. 5. Developmental-stage pyramids for *Triatoma infestans* (left side) and *Rhodnius prolixus* (right side). The base represents a pool of nymphs I, II, III and IV, the intermediate section, nymphs V, and the upper section the adult population. The numbers associated with each section are the percentage of the respective developmental-stage class in the total population. Each pyramid shows (from the top to the bottom) the population structure every 30 days after entering the tenth year of simulation.

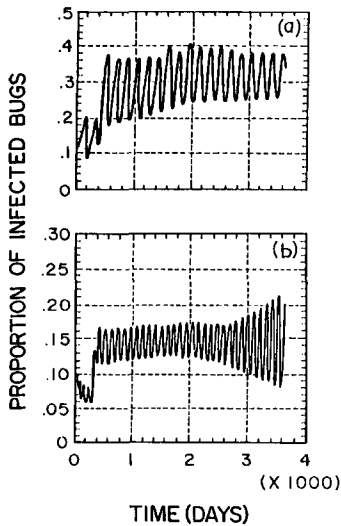


Fig. 6. Proportion of infected bugs [(a) *Triatoma infestans* and (b) *Rhodnius prolixus*] in house type 1 with one initial infected dog.

R. prolixus about four per year, with adults lagging after nymphs by 150 and 75 days, respectively.

During the oscillations the population development-stage pyramid changes (Fig. 5). In general, adults represent a small fraction of the total population (between 2% and 5%).

Although the population was divided only into eggs, nymphs and adults, knowledge of the average development time of the five nymphal stages for each vector species allowed the grouping of densities by nymphal stages for the purpose of showing changes in the developmental structure of the population with time. The bug population's infection fluctuates, oscillating between 30% and 60% for *T. infestans* (Fig. 6a) and between 5% and 20% for *R. prolixus* (Fig. 6b).

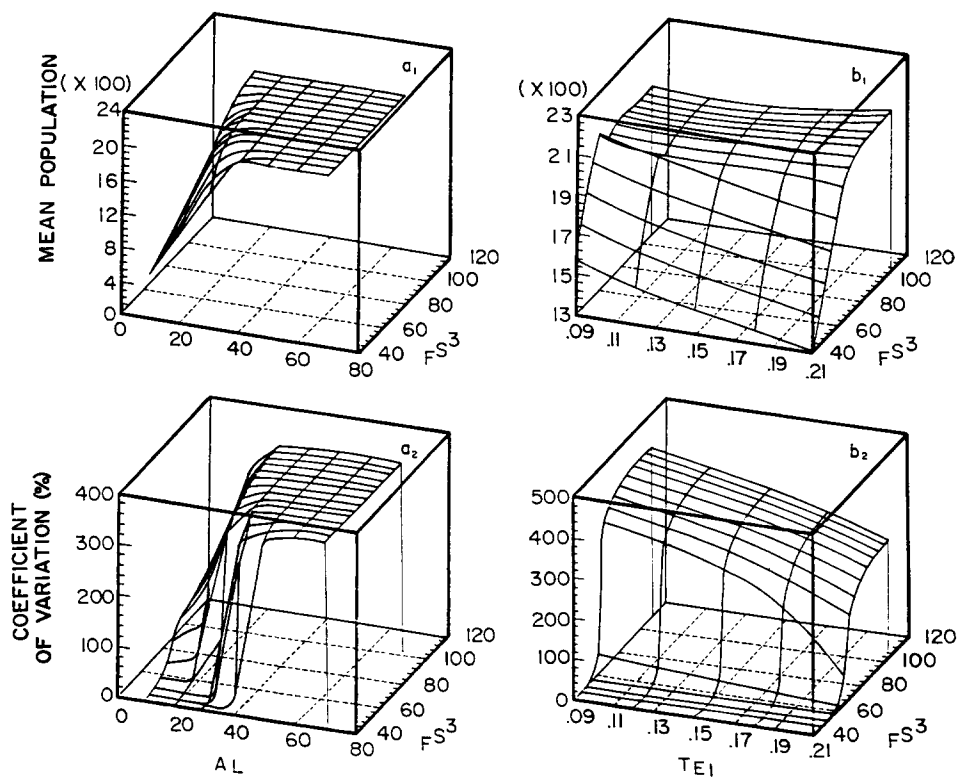


Fig. 7. Effect of simultaneous changes in AL (number of hosts) (a) or TE_1 (insect adult house emigration rate) (b) and FS^3 (threshold nymphal density at which irritation of the host starts), on the stability behavior of simulated *Rhodnius prolixus* populations. Subindices 1 and 2 represent the average stable population and its coefficient of variation, respectively.

SENSITIVITY ANALYSIS

The stepwise regression of the 81 runs for sensitivity analysis showed that the two basic mortality rates (TM1 and TM2) had a negligible effect on the vector's mean stable population size (MSP) and its coefficient of variation (CV), leaving only the mortality density-dependent parameter (FS3) and the natality rate (TNATCH) as the most sensitive parameters. The standardized partial regression coefficients for TNATCH and FS3 were 0.807 and 0.348 for MSP, and 0.850 and 0.054 for CV, respectively. However, having observed from previous simulations that the total number of hosts (AL) and the emigration rate (TE1) had an important effect on the MSP, they were also incorporated into simultaneous combinations with TNATCH and FS3 in a second, more detailed, sensitivity analysis.

The parameter values used for both species were (each triplet represents the minimum, the maximum, and the step of change in that order): for FS3,

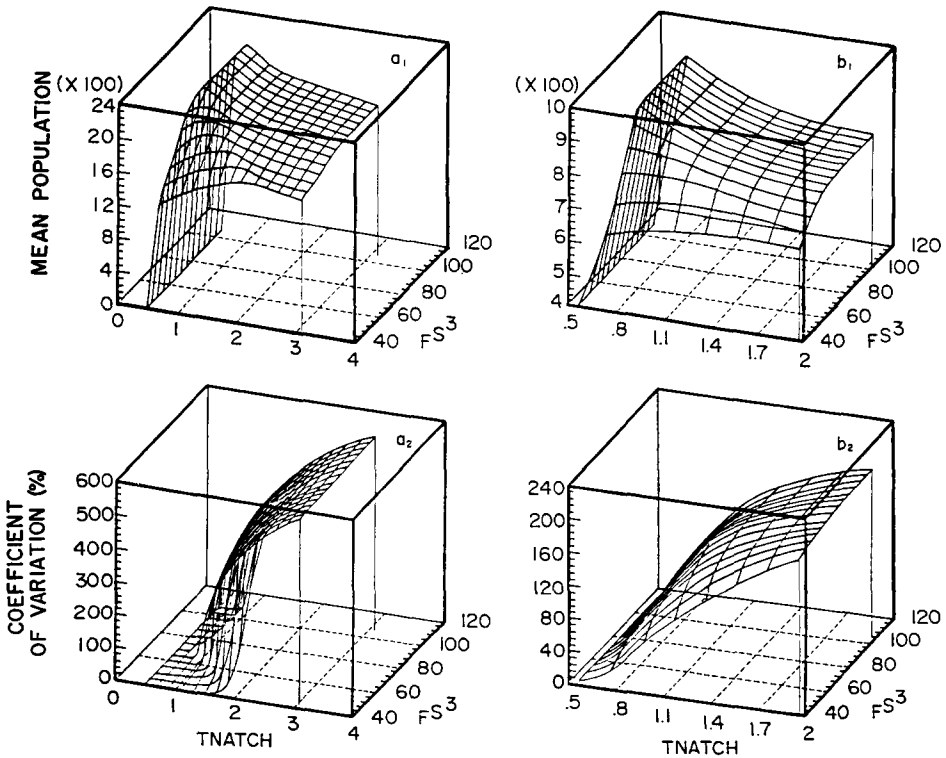


Fig. 8. Effect of simultaneous changes in TNATCH (natality rate) and FS3 (threshold nymphal density at which irritation of the host starts) on the stability behavior of simulated *Rhodnius prolixus* (a) and *Triatoma infestans* (b) populations. Subindices 1 and 2 represent the average stable population and its coefficient of variation, respectively.

40, 105, 5; for TE1, 0.12, 0.18, 0.03; for AL, 10, 70, and 10. As fecundity is different for each species (Table 2), the TNATCH values used for *R. prolixus* were: 0.5, 3.1, 0.2; and for *T. infestans*, 0.57, 1.97, 0.2. This gives 2058 combinations for *T. infestans* and 4116 combinations for *R. prolixus*, giving a total of 6174 runs of the simulation model.

The changes in MSP and CV for simultaneous variations of FS3 and AL, and also in FS3 and TE1 for *R. prolixus* are shown in Fig. 7a and b, respectively. They display a steep interaction when FS3 and AL vary simultaneously, but a smooth one for variations in FS3 and TE1. The simultaneous variations in FS3 and TNATCH also show a steep interaction in the MSP and CV results for *R. prolixus* (Fig. 8a), but a smooth one for *T. infestans* (Fig. 8b).

In all cases there is evidence that CV (the coefficient of variation, here used as an indicator of stability behavior) jumps from null values to relatively high ones (except in Fig. 8b), suggesting a change in the stability

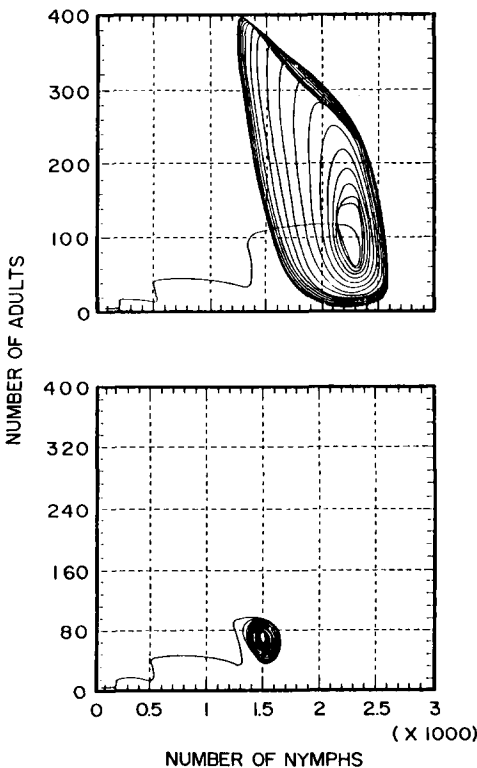


Fig. 9. Phase diagrams of nymph and adult numbers of *Rhodnius prolixus* simulated populations for FS3 (threshold nymphal density at which irritation of the host starts) values of 100 (upper graph) and 50 (lower graph).

behavior from a stable point to a limit cycle. This change in behavior is better exhibited if population values are displayed in a phase diagram of nymphs against adults, as shown in Fig. 9 for changes in FS3 from 50 to 100 in *R. prolixus*. With all other parameters in their standard values, FS3 = 50 produces a phase diagram with a 'closing-up' spiral trajectory indicating an equilibrium point around 1500 nymphs and 65 adults; the trajectory of the phase diagram for FS3 = 100 shows a progressively 'opening-up' spiral until it reaches a limit cycle confined to about 1300–2600 nymphs and about 10–400 adults.

DISCUSSION

Our model shows that populations of both insect species fluctuate with periodicities that reflect their development times: *R. prolixus*, with a total development time (eggs, nymphs, and pre-reproductive adults) of 90 days has about four peaks per year, while *T. infestans*, with a total development time of 170 days, has about two cycles per year.

The development time is also associated with the temporal alternation of developmental stages' abundances: the peak of the adult population lags behind the nymphal peaks in proportion to the development time of each species (cross-correlation analysis shows an average lag of 73 and 132 days for *R. prolixus* and *T. infestans*, respectively). This periodic change in the developmental-stage structure also affects the percentage of infected bugs; these percentages fluctuate with peaks of infection that coincide with peaks of adult bug populations. This is so because the acquisition of the infection by the bugs is a time-cumulative process: the percentage of infected bugs increases with developmental stage.

The asymmetry of the population oscillation seems to be related to fecundity: the growing arm is much steeper than the falling one in the oscillation of the nymph population in the case of *R. prolixus* with a fecundity of 1.3 eggs per female daily, while it is symmetric in the case of *T. infestans* with a fecundity of 0.77 eggs per female.

The densities of the simulated populations show two types of behavior: a stable equilibrium point and a limit cycle. The limit-cycle behavior is determined by the non-linear natural mortality function. However, as suggested by sensitivity analyses, *the change in behavior* results from the interaction between the two sources of mortality: the natural mortality (a sigmoid density-dependent function related to the carrying capacity) and the starvation mortality (a linear density-dependent function related to host irritation). When the parameter FS3 of the starvation-mortality linear function has a low value (e.g., 55–65 for *R. prolixus*), population regulation takes

place at a population density that does not allow the action of the non-linear natural-mortality function.

It is known that the switch between a stable point and an oscillatory behavior is modulated by both the fecundity and the development time (Hastings and Constantino, 1988). *Rhodnius prolixus* has egg and nymphal development times shorter and fecundity larger than *T. infestans*; the differences in the population stability behavior of the two species analyzed here probably reflect these two biological parameters.

This knowledge about the stability behavior of these two species vectors will be of value in the application of models for the design of the optimum control strategy of Chagas' Disease transmission; controls should aim at shifting populations to a stable point equilibrium (thus avoiding population explosions) at their lower possible values.

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