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## Flight Initiation of *Triatoma infestans* (Hemiptera: Reduviidae) Under Natural Climatic Conditions

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### Abstract

Flight dispersal of *Triatoma infestans* Klug is probably the most important mechanism for house reinfestation at a village scale after residual spraying with insecticides. The aim of the current study was to estimate the flight initiation probability of field-collected *T. infestans* and to assess how this probability was affected by sex, adult age, partial bloodmeal, and the presence of a host inaccessible for feeding. Four experimental series, each consisting of three to six consecutive nights and repeated measurements of flight initiation on each individually marked bug, were carried out in experimental huts inside closed cages under natural climatic conditions. We demonstrate that flight initiation probability of *T. infestans* is much higher than previously reported, responds to temperature in a sigmoid manner, and is higher in females than males, and that the frequency distribution of the number of flights per individual is highly aggregated in female and male bugs. The age of adults had strong effects on flight initiation, whereas the presence of an inaccessible host and a partial bloodmeal exerted no significant effects in models controlling for the effects of bug weight-to-length ratio. The high flight potential found is consistent with the rapid changes in reinfestation patterns observed in the field. The present estimates of flight probabilities and the identification of factors modifying them provide essential knowledge for modeling reinfestation patterns and for improving control strategies of *T. infestans*.

### Keywords

flight initiation; Triatominae; Chagas disease; reinfestation

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THEORETICAL AND EMPIRICAL DATA suggest that flight dispersal by *Triatoma infestans* Klug, the main vector of Chagas disease in South America, is the most important mechanism for reinfestation of houses at a village scale after insecticide spraying (Schofield and Matthews 1985, Cecere et al. 2004, Vazquez-Prokopec et al. 2004, unpublished data; Ceballos et al. 2005). Yet a key reference source disregards flight dispersal in favor of passive transport by humans as a major driver of local reinfestation (WHO 2002). Such misconception probably arose from the typical nocturnal activity and sporadically observed flights of *T. infestans*. *T. infestans* may easily fly >550 m (Schofield et al. 1992) or reach 1,500 m (Schweigmann et al. 1988) in an open field, and it may sustain tethered flights for >20 min at speeds of 2 m/s (Ward and Baker 1982).

Flight initiation is associated with low nutritional status (estimated by weight-to-length ratio, W/L), high temperatures, and low wind speed (Lehane and Schofield 1982, Lehane et al. 1992, Vazquez-Prokopec et al. 2004, unpublished data). Flight initiation is positively associated with adult age for up to 40-60 d and then falls to lower constant levels (Lehane and Schofield 1982). In laboratory experiments, Williams and Schofield (1985) reported higher proportions of female *T. infestans* flying, whereas Lehane et al. (1992) found no significant differences between sexes. Although triatomine bugs are known to be attracted by host odors and radiant heat (Lazzari and Núñez 1989, Taneja and Guerin 1995), there are no published reports on the effects of these attractants or a live host on flight decision. Previous evidence suggests that sex would have negligible effects on flight initiation, whereas the presence of an inaccessible host and a partial bloodmeal would exert negative effects, and age would increase flight probability during the first 5 wk after adult emergence.

Decision-making processes, including those involving the triggering of complex motor displays, depend on the integration of information provided by different senses as well as the general motivational level of the animal (McFarland 1971). Addressing these behaviors requires analyzing responses under conditions that mimic natural situations as close as possible (Lorenz 1959). However, previous studies on *T. infestans* flight behavior were conducted under artificial test conditions and usually with triatomines reared in the laboratory for many generations (Lehane and Schofield 1981, 1982; Lehane et al. 1992; Schofield et al. 1992; McEwen et al. 1993). The behavior of laboratory bugs and natural populations may differ significantly, especially because size, weight, shape, and antennal sensilla have been shown to vary between them (Jaramillo et al. 2002, Catalá et al. 2004, Vazquez-Prokopec et al. 2004).

The aim of the current study was to assess experimentally the flight initiation probabilities of field-collected *T. infestans* under natural climatic conditions and how these probabilities were associated with sex, adult age, a recent partial bloodmeal, and the presence of a host inaccessible for feeding, while controlling for W/L ratio effects. Individual behavioral variability also was assessed by means of a repeated measures design.

## Materials and Methods

### Field Site

The experiments were carried out at the National Vector Control Coordination (NVCC) field station located in Santa María de Punilla (31° 14' S, 64° 28' W), Province of Córdoba, Argentina, which lies within the distribution range of *T. infestans* and has been used for investigations on bug population dynamics under natural climatic conditions (Cecere et al. 2003). The annual mean temperature is  $\approx 15^{\circ}\text{C}$ , with absolute maxima reaching  $40^{\circ}\text{C}$  in summer. Annual rainfall ranges between 500 and 600 mm from November to March.

### Insects

For a pilot assay, adult *T. infestans* from a 2-yr-old colony kept at the insectary of the NVCC for three to four generations were used. This colony originated from wild-caught bugs from the Department of Cruz del Eje, Province of Córdoba, and was regularly fed on chickens. The adults used were 5-20 d old and were not fed after the final molt.

For the experiments, 360 adults and  $\approx 500$  fourth and fifth instars of *T. infestans* were collected in February 2004 from peridomestic sites in neighboring villages (Km 34, Km 40, Invernada Norte and La Loma) located in the Department of Figueroa (27° 23' S, 63° 29' W), Province of Santiago del Estero, Argentina. Bugs were collected by searches in chicken nests, kitchens, and storerooms and then transported to the field station in plastic jars with filter paper.

## Experimental Design

Each experimental device (Fig. 1) consisted of a small hut (30 cm in width, 25 cm in height) inside a cage made of plastic mosquito netting mounted on a metal frame, and covered with additional mosquito netting for further protection. Each hut had a 30-cm-wide, 5-cm-thick roof of shrubs (*Larrea* sp.) positioned on two logs of blackwood, *Acacia melanoxylon* R. Br. ex Ait. f., and tied with wire. The roof rested on two mud bricks (the hut walls) and was covered by a 25 by 25cm square piece of black nylon and two mud bricks. A surrounding barrier was 5 cm apart from the hut and consisted of a 15-cm-high aluminum plate that could not be climbed by the bugs. In the inner side of the cage roof and 15 cm away from the walls, another 7-cm-high aluminum plate prevented fliers from walking over the hut and falling back into it. Four pleated corrugated cardboard refuges (23 by 10 by 6 cm) on the floor close to the cage walls and another four refuges (40 by 5 by 5 cm) on the top corners provided shelter for fliers. A data logger (HOBO, Onset Co., Bourne, MA) placed inside each hut registered temperature (precision  $\pm 0.7^{\circ}\text{C}$ ) and relative humidity (precision  $\pm 5\%$ ) every 15 min. The cages were in a row, almost 3 m apart, and 10-20 m away from a chicken house and an inhabited house.

The pilot assay was conducted to test whether the experimental device was effective for registering *T. infestans* flight initiation and to assess the effect of marking on flight initiation. About half of the bugs were marked on the pronotum with two dots of acrylic paint (Liquitex and Alba, Buenos Aires, Argentina), which exerted no adverse effects on the survival of *T. infestans* (Cecere et al. 2003). A group of *T. infestans* was released in each of two huts at 1300 hours and recovered the next morning at 1000 hours. Bugs recovered beyond the aluminum barrier were considered to have initiated flight. In total, 48 males and 42 females were released on 21 January and 70 males and 64 females on 22 January. An infrared videocamera (900 nm) placed in one of the top corners of a cage recorded bug activity in the exterior of the hut and within 20 cm around the aluminum barrier on the floor, from  $\approx 2000$  to 0400 hours. All the bugs that left the hut were observed to do so flying and none of them returned, thus demonstrating the effectiveness of the experimental hut design for present purposes. No significant effects on flight initiation of the acrylic paint mark were found (data not shown).

Four experimental series (A-D) were conducted (Table 1). Each series consisted of four groups of 31-41 adult *T. infestans* with a sex ratio of two males per female, as in the original field collection. Bugs were individually identified with two dots of acrylic paint (six colors) in two of five different positions on the pronotum. Two of the four huts harbored a male mouse kept in a glass jar closed with metal mosquito netting to prevent the bugs from reaching the host. A group of bugs was released in each of the huts at  $\approx 2000$  hours. For the next two nights, a mosquito net held to the aluminum barrier prevented bugs from leaving the hut either by walking or flying, allowing the bugs to adapt to the new environment. After the two confinement nights, the mosquito net was removed and during the next three to six measurement nights (depending on the series; Table 1), bugs were allowed to fly out of the hut. After each measurement night, the color mark of the bugs found beyond the aluminum fence was registered early in the morning. The bugs were immediately returned to the hut, except after the last night of each series when all bugs were recovered. In series D, most parts of the huts were affected by a heavy rain on the second confinement night; some of the wet mud bricks were replaced by dry bricks after the second night of measurement.

All recovered bugs from series B-D were individually weighed on an electronic balance (Shimadzu Libror, AEG-220, Duisburg, Germany) (precision  $\pm 0.1$  mg) and measured from clypeus to abdominal tip with a hand-held vernier caliper (precision  $\pm 0.05$  mm). The W/L ratio was assumed approximately constant during the measurement nights because several days had passed since the last bloodmeal (Lehane and Schofield 1982). Mortality was 1.4% (2/144) in series B, 0% in series C, and 1.5% (2/133) in series D. In series A, bug nutritional status

was only estimated qualitatively (Montenegro 1983, Ceballos et al. 2005), and mortality was not recorded.

## Data Analysis

Repeated measures multiple logistic regression was used within each series to assess the effects on the binary response variable (bug flying on a given night) of sex, W/L ratio (continuous variable), a partial bloodmeal (categorical variable, series D), adult age (categorical variable with four levels, series C), and the presence of a mouse not accessible for feeding (categorical variable, series B-D). All replicates within a series were pooled for analysis because no significant effect of each particular setup was found. Unless stated otherwise and because of the low temperatures registered in series A and during the first two nights of series D (Table 1), averages and regressions were calculated only for all three measurement nights of series B and C and the last four measurement nights of series D. Generalized estimating equations method (GEE) was used to estimate and control for the correlation between repeated measures (Liang and Zeger 1986). The group variable was the individual bug and the time variable was the measurement night. An unstructured correlation matrix and the robust variance estimator were used. Differences in the proportions of flight initiation between the pilot assay and series B-D were tested for using repeated measures multiple logistic regression as stated above; the independent variables were sex and the specific series (the pilot assay being the reference category). To test whether flight initiation probabilities differed among individual bugs of the same sex, the observed frequency distribution of the number of nights that each bug flew was compared with the expected distribution under the null hypothesis that the probability was the same for all nights and bugs. The difference in the flight proportions between nights for each series and sex was evaluated using a chi-square test. All analyses were run on Stata 7.0 (StataCorp 1999).

## Results

In the pilot assay with insectary bugs, an average of 30% of male and 56% of female *T. infestans* initiated flight each night (Fig. 2). For series B-D, an average of 43% (range 25-52%) of 255 male and 67% (range 54-76%) of 159 female bugs collected in the field initiated flight each night. Female bugs were consistently more likely to initiate flight than males in all nights and series. Logistic regression analysis showed that the bugs from the pilot assay flew significantly less frequently than the bugs from series B ( $P < 0.001$ ) and D ( $P = 0.01$ ) and marginally less frequently than bugs from series C ( $P = 0.07$ ).

Flight initiation was practically absent up to 23° C at sunset (2000 hours) (series A and the first two nights of measurement of series D; Table 1), increased sharply above 23° C and remained fairly constant with increasing temperatures above 23° C (Fig. 3). This suggests an upper limit or asymptote of ≈50% for males and 75% for females. In the pilot assay, the temperature at sunset was 24.5° C on both nights. Wind speed was always negligible.

Table 2 presents the multiple regression analysis assessing the effects of different factors on flight initiation. Female bugs were consistently more likely to initiate flight than males in series B-D (Table 2) and the pilot assay ( $P < 0.01$ ). In series C, the significant interaction between sex and age was consistent with the main effects observed in series B and D, with females showing a higher flight initiation probability than males (Fig. 4). Therefore, age was analyzed for each sex separately while controlling for W/L effects. Taking the most abundant age group (i.e., 3-wk-old bugs) as the reference class, 1- and 2-wk-old males initiated flight significantly less frequently than 3-wk-old males (OR, 0.16; 95% CI, 0.03-0.78), and these did not initiate flight significantly more often than 4-(OR, 1.15; 95% CI, 0.38-3.41) and 5-wk-old males (OR, 1.95; 95% CI, 0.73-8.26). Only 4-wk-old females had a flight initiation proportion significantly

different from 3-wk-old females (OR, 6.89; 95% CI, 2.27-20.92). The presence of an inaccessible host exerted no significant effects on flight initiation in any series (Table 2).

The effects of the W/L ratio were only significant in series C (Table 2). In series D, W/L effects were significant only when the effects of a partial bloodmeal were removed from the regression model (data not shown). The absence of a clear negative effect of the W/L ratio on flight initiation is probably because of the narrow, low range of W/L values in the study bugs. Comparing the current W/L distribution with that of a natural population of *T. infestans* with a general poor nutritional status evidences how starved all the bugs used were (Fig. 5).

The recent partial bloodmeal increased moderately the bug W/L ratio (mean  $\pm$  SD for fed bugs,  $8.6 \pm 1.3$  mg/mm; unfed bugs,  $6.9 \pm 0.9$  mg/mm) (analysis of variance [ANOVA] of recent bloodmeal nested in sex,  $F = 43.4$ ;  $df = 1, 127$ ;  $P < 0.001$ ) and decreased flight initiation chances only when the effects of the W/L ratio were removed from the regression model (data not shown). To avoid the unbalanced numbers of bugs between the extreme W/L classes of recently fed and unfed bugs, only bugs with W/L ratios between 6 and 9 mg/mm were included in another regression analysis (Table 2). Neither W/L ratios nor a recent partial bloodmeal had significant effects on flight initiation in this subset of bugs.

The observed frequency distributions of the number of nights that a bug flew differed significantly from the expected values (assuming the same flight probability for all nights and bugs within a series) for both sexes in all series (in all cases,  $\chi^2 > 45$ ,  $df = 3$ ,  $P < 0.001$ ) (Fig. 6). No significant differences were found in flight initiation between nights within the same series ( $P > 0.15$ ; Fisher's test), except for males in series D ( $P = 0.002$ ), probably because of the lower temperature during the third night of measurement. Therefore, the flight probability differed significantly among individual bugs of the same sex and series, providing evidence for the existence of bugs that were clearly fliers or nonfliers. Female bugs presented always higher proportions of always-fliers and lower proportions of never-fliers than males.

## Discussion

Our study demonstrates that flight initiation probability of *T. infestans* is much higher than previously reported, responds to temperature in a sigmoid way, is higher in females than males and that the frequency distribution of the number flights per individual is highly aggregated in females and males. The probabilities of flight initiation here recorded for field-collected *T. infestans* exceed all previous reports, even though most of these earlier studies were conducted under higher temperatures (Table 3). Differences in size, shape, weight, and antennal sensilla between field and insectary-reared triatomines (Jaramillo et al. 2002, Catalá et al. 2004, Vazquez-Prokopec et al. 2004) suggest that these bugs also may present behavioral differences. In fact, the insectary bugs used in the pilot assay flew significantly less frequently than the field-collected bugs, despite having similar qualitative nutritional status and environmental conditions. The observed constancy of flight initiation proportions within a given temperature range suggests that differences in protocols and experimental conditions (e.g., uncontrolled variation in device materials, nearby lights and hosts) across series were of negligible importance. Thus, field *T. infestans* seem more prone to fly than bugs reared for successive generations in glass jars and subject to inbreeding effects. Other factors (availability of space and food, feeding frequency, and constancy of environmental conditions) also may be contributing to the observed differences.

The apparent temperature threshold for flight initiation of  $\approx 23^\circ\text{C}$  is consistent with light trap collections of *T. infestans* (Vazquez-Prokopec et al., unpublished data) and contrasts with the reported linear relationship between flight and temperature (Williams and Schofield 1985), although reanalysis of the data showed it to be also consistent with a sigmoid relationship (C. J. Schofield, personal communication). Similar findings in other triatomines (Ekkens 1981)

and various insects lend more support to a threshold response than to a linear relationship between temperature and flight initiation. Further work is needed to establish more precisely the existence of a temperature threshold and the factors affecting it.

The consistently higher flight initiation probabilities for female bugs agree with all trends reported in previous studies that discriminated between *T. infestans* sexes, except for one study (Lehane et al. 1992), although these were not tested for statistical significance (Table 3). Moreover, a replicated field experiment found that 82% of female *T. infestans* and 29% of males fled away from open, inhabited chicken coops after 2 mo (Canale and Carcavallo 1988). These findings contrast with the male-biased light trap collections of *T. infestans* (Vazquez-Prokopec et al. 2004, unpublished data), but this apparent contradiction disappears when the sex ratio of the putative bug sources is considered.

The peak flight initiation in females aged 4 wk and males older than 3 wk is notably consistent with most previous results, despite differences in the insects' origin and experimental setup (Lehane and Schofield 1982, Ward and Baker 1982). The only exception (Lehane et al. 1992) may be explained by the old bug colony used. In addition, the present results suggest an interaction effect between age and sex. The peak flight probability around three weeks of age as adults in *T. infestans* coincides with a two-fold increase in mass of flight muscles and a five-fold increase in their lipid content (Ward et al. 1982). In some heteropterans, the histolysis of flight muscles occurs only in females, increases with age, is usually stimulated by feeding and copulation, and is coupled with oogenesis (Nair and Prabhu 1985). These physiological changes may be the mechanisms underlying the observed interaction between age and sex on flight initiation.

Blood ingestion on its own did not modify flight initiation probabilities under our experimental conditions. A recent partial bloodmeal exerted no effects on flight initiation 5-10 d after feeding, whereas fully engorged *T. infestans* did not initiate flight until 10-15 d after feeding, when body weight had declined sufficiently (Lehane and Schofield 1982). These results jointly suggest that the size of the partial bloodmeal was not sufficient for producing a significant increase in W/L above 10 to 11 mg/mm, which would deter bugs from flying (Lehane et al. 1992), because weight consistently limits take-off in a wide spectrum of species (Marden 1987). Regarding physiological effects of blood ingestion, the time elapsed since partial feeding may not have been sufficient for a change in metabolism to occur, as suggested by results on fat body mass and lipid content in *Panstrongylus megistus* (Burmeister) (Canavoso and Rubiolo 1998, Canavoso et al. 1998). The relative role of mechanical (e.g., weight increase, crop or body wall distension) and physiological factors on flight initiation requires further research.

Although mice attract bugs under laboratory (Taneja and Guerin 1995) and field conditions (Noireau et al. 1998), the presence of an inaccessible mouse had no effects on flight initiation in the current study. The most conservative explanation might be that stronger stimuli with positive effects, such as the unavoidable manipulation that bugs experienced since field collection, the novel environment, surrounding sensorial cues, and bug density, masked the effects of host presence. Alternatively, if none of these or other factors were involved, the results would suggest that the sensorial cues associated with an inaccessible host have no effects on bug flight decision.

The distribution of individual flight initiation was highly aggregated, with most of the bug population divided into fliers (bugs with a very high probability of initiating flight) and nonfliers (those with a very low or null probability of flying) across all experimental series. This also explains the upper limit reached by flight initiation proportions with increasing temperature (Fig. 4). Sex, age, or W/L variations could not discriminate between fliers and

nonfliers. Previous studies that reported on flier and nonflier bugs only assessed for differences in W/L of *T. infestans* (Lehane and Schofield 1982) or glycerol-3-phosphate dehydrogenase activity (an essential enzyme for obtaining energy) in *P. megistus* and *Triatoma sordida* (Stål) (Soares and Santoro 2000). Other factors also may influence flight initiation in *T. infestans*.

The high probabilities of flight initiation found, especially in females, demonstrate that *T. infestans* has a higher flight potential than previously recognized. This supports the importance of flight dispersal as a major driver of the reinfestation process after insecticide spraying at a village-wide scale. Moreover, the observed effects of temperature and age may assist in identifying an appropriate time window for flight dispersal and founding of new bug colonies. Temperatures >23°C and wind speed <5 km/h are necessary for flights to occur, but bugs also need to be light enough, either because of starvation or lack of a full bloodmeal. When these conditions combine together with maximum abundance of adult bugs aged 3-5 wk old, peak flight probabilities should be expected. Determining this time window could assist in the optimal timing of bug control operations.

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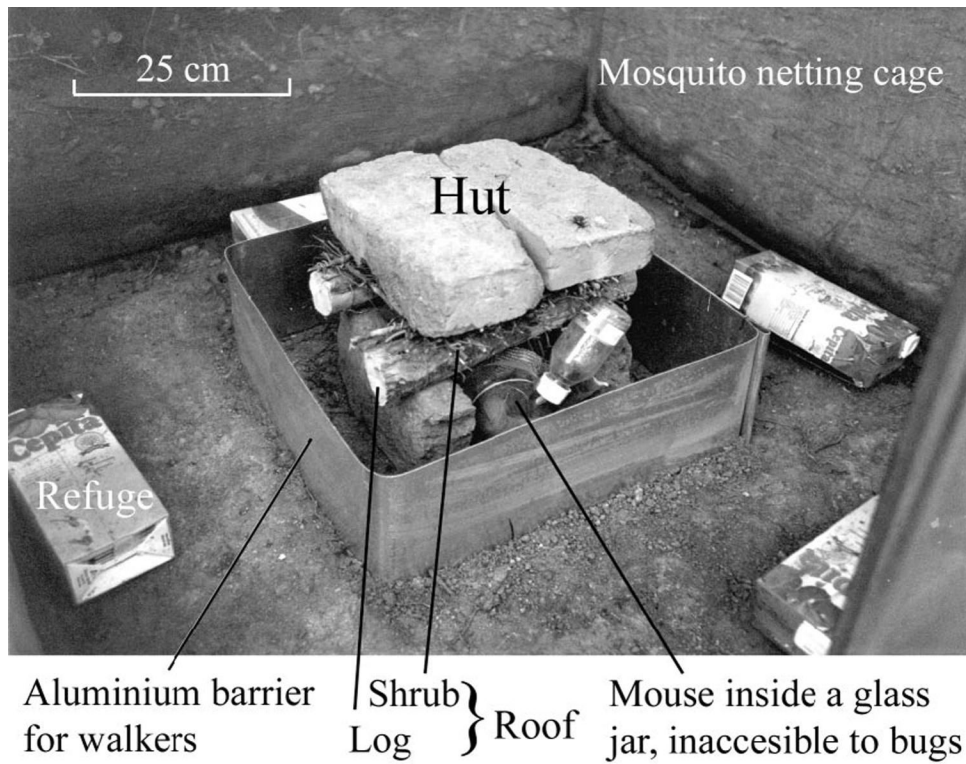
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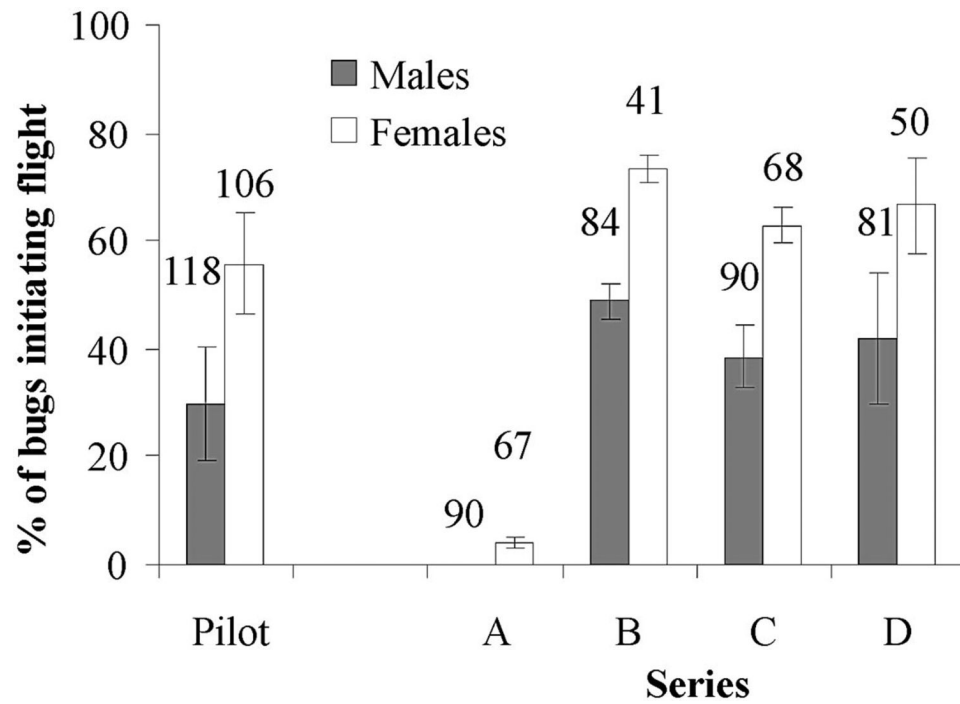
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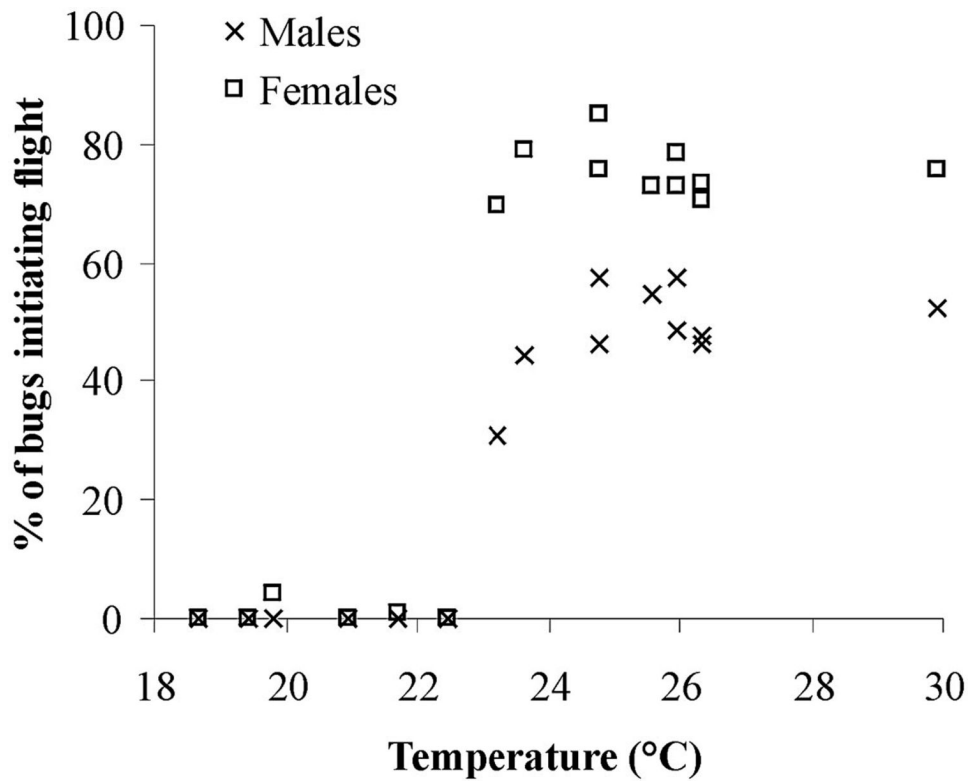




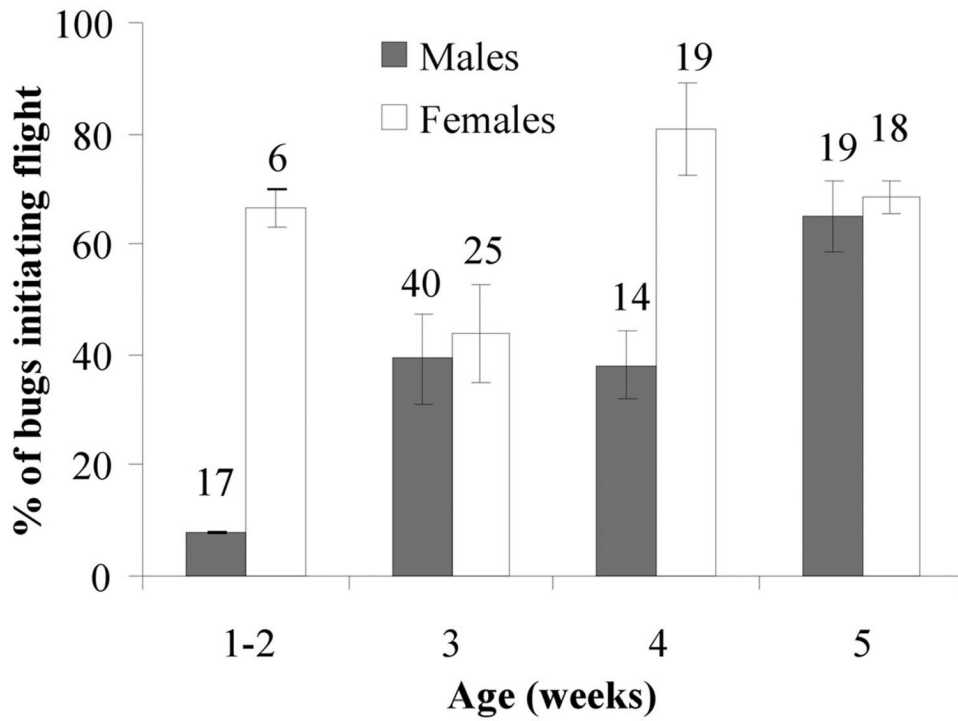
**Fig1.** Experimental device for registering flight initiation of *T. infestans* under natural climatic conditions.



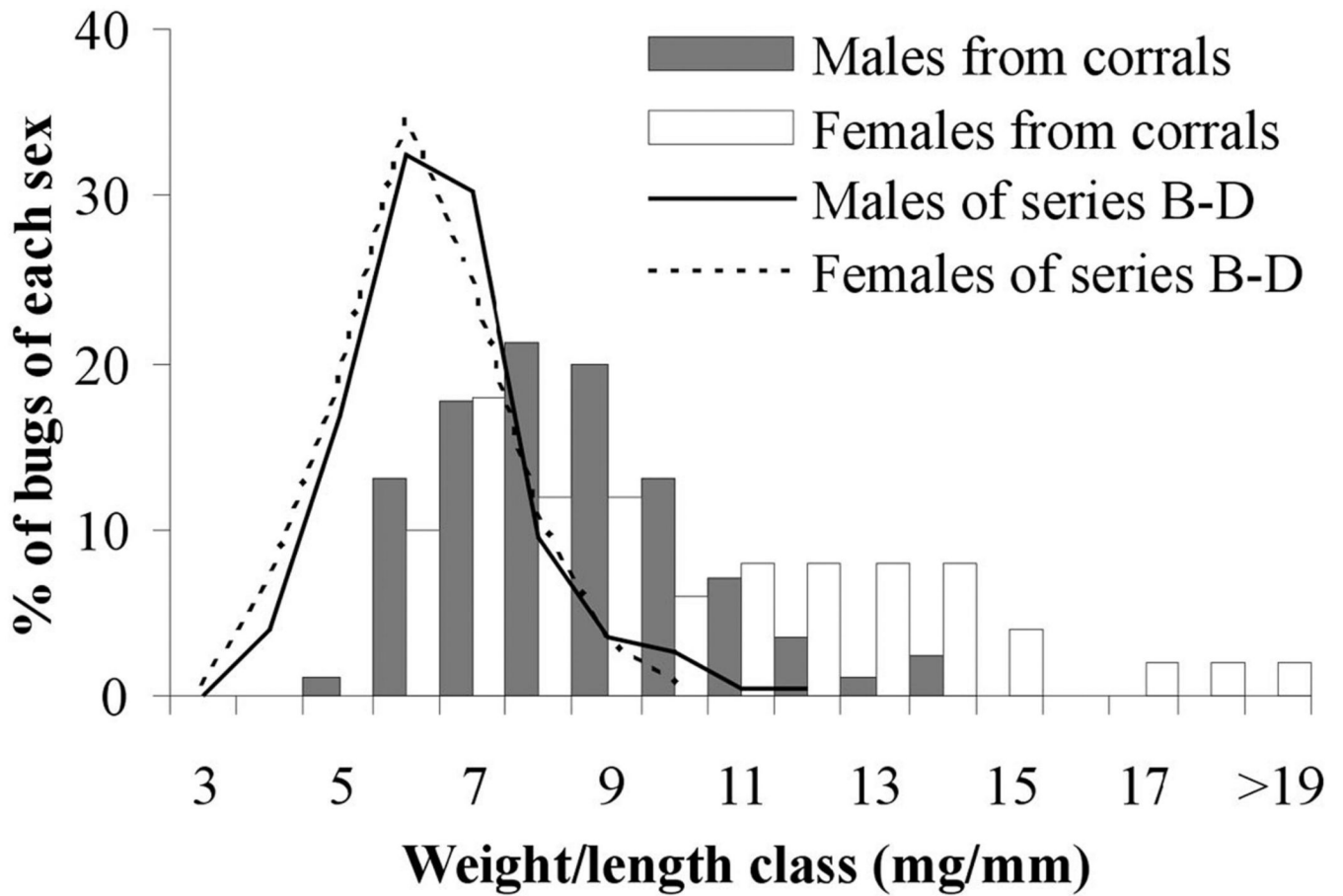
**Fig2.** Sex-specific average percentage of *T. infestans* that initiated flight in the pilot assay and the four experimental series. The numbers above the bars indicate the total number of bugs tested in each series. Lines indicate  $\pm 1$  SD.

**Fig3.**

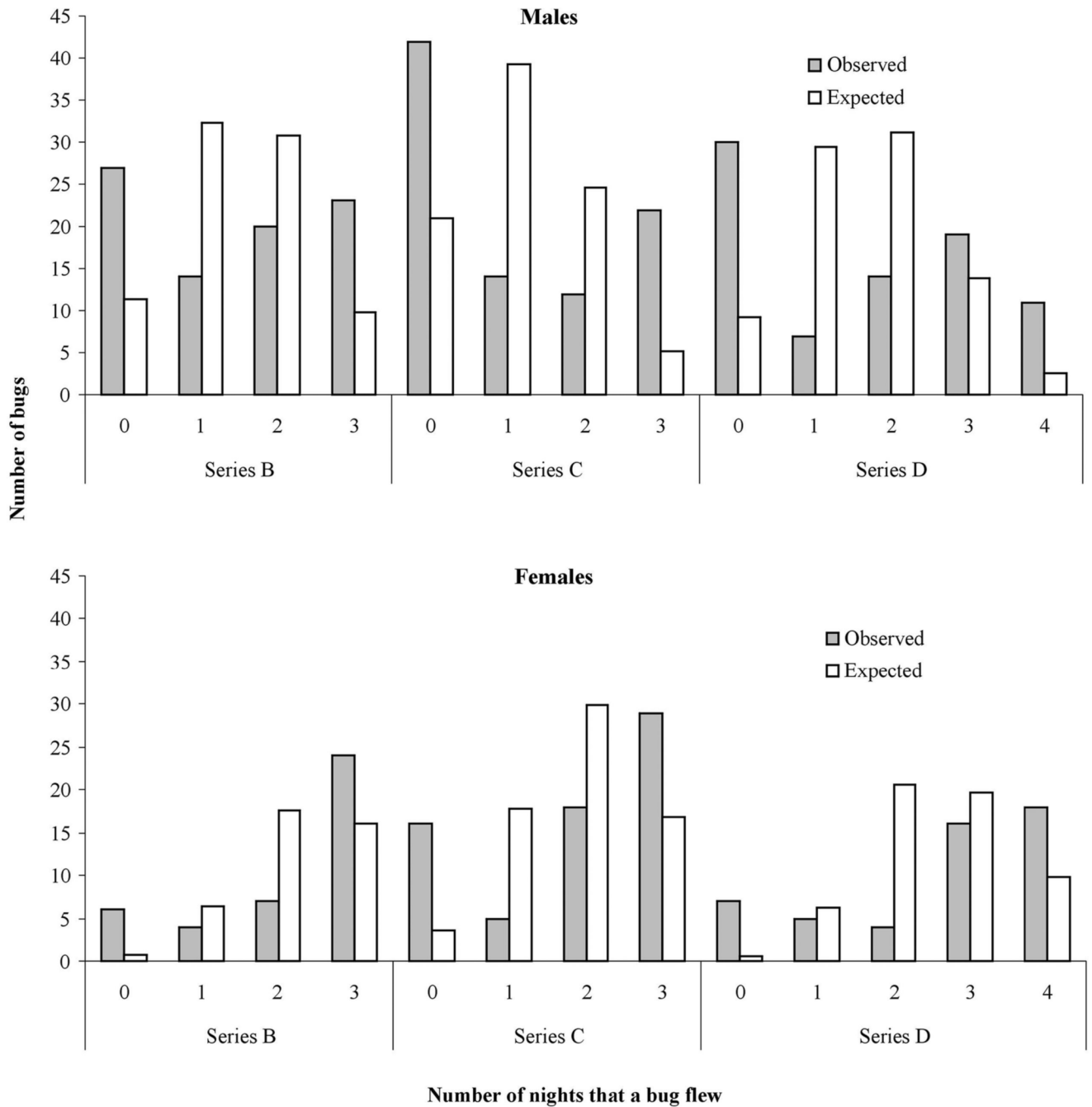
Flight initiation of field-collected *T. infestans* according to the temperature at sunset for every measurement night of all experimental series (A-D). The values shown correspond to relatively comparable bugs: all bugs from series A and B, bugs  $\geq 4$  wk old from series C, and unfed bugs from series D.



**Fig4.** Average flight initiation of field-collected *T. infestans* according to sex and age of adults in series C. The numbers above the bars indicate the total number of bugs tested in each class. Lines indicate  $\pm 1$  SD.



**Fig5.** Sex-specific W/L distribution of the *T. infestans* bugs used in series B-D (lines) compared with the distribution corresponding to a bug population from goat and pig corrals (bars), typically with a poor nutritional status at the end of summer in northern Argentina (Ceballos et al. 2005).



**Fig6.** Sex-specific observed and expected frequency distribution of the number of nights that each individual *T. infestans* bug flew. Expected values were calculated under the hypothesis that flight probability was the same for all bugs of the same sex over all nights within a series.

**Table 1**  
 Details of the four experimental series carried out for registering flight initiation of field-collected *T. infestans*

Series	No. of bugs	Release-recovery date	Nights of measurement	Maximum daily temp	Daily temp at sunset	Bug characteristics
A	156	15-22 Feb.	5	16-25	19-23	Adults used 5 d after field collection and kept unfed since then As in series A, used 10 d after collection
B	142	22-27 Feb.	3	28-34	26-30	Recruited from field-collected fifth instars; used 1 mo after being fed to repletion on chickens; adult age of each bug known with a 1-wk precision
C	158	24-29 Mar.	3	30-31	26-30	Previously used in series A; fully engorged 15 d after collection; after 1.5 mo of starvation, onethird of females and males were again allowed to feed partially on chickens for $\approx$ 5 min
D	131	29 Mar.-6 April	6	21-22 (first and second night) 25-28 (third-sixth night)	19-20 (first and second night) 23-25 (third-sixth night)	

Temperatures express the range observed for the measurement nights in each series.

**Table 2**  
Repeated measures logistic regression analyses of factors associated with flight initiation of field-collected *T. infestans* under

Series	Independent variable	Odds ratio $\pm$ SE	P (z)	95% CI	P (Wald)
B	Sex	0.33 $\pm$ 0.11	0.001	0.17-0.64	
	W/L	0.91 $\pm$ 0.11	0.47	0.72-1.17	
C	Host	1.41 $\pm$ 0.44	0.27	0.77-2.58	0.007
	Sex	0.85 $\pm$ 0.37	0.72	0.36-2.01	
	W/L	0.48 $\pm$ 0.08	<0.001	0.35-0.65	
	Age 1-2 wk	0.16 $\pm$ 0.14	0.32	0.03-0.86	
	Age 4 wk	1.16 $\pm$ 0.64	0.79	0.39-3.45	
	Age 5 wk	1.98 $\pm$ 1.04	0.20	0.70-5.55	
	Sex $\times$ age 1-2 wk	13.2 $\pm$ 14.6	0.02	1.46-116	
	Sex $\times$ age 4 wk	5.96 $\pm$ 4.40	0.02	1.40-25.4	
	Sex $\times$ age 5 wk	0.99 $\pm$ 0.78	0.99	0.21-1.64	<0.001
	Host	0.98 $\pm$ 0.18	0.93	0.69-1.41	
D (all bugs)	Sex	0.38 $\pm$ 0.11	0.001	0.22-0.67	
	W/L	0.82 $\pm$ 0.12	0.17	0.62-1.09	
	Partial meal	0.62 $\pm$ 0.23	0.20	0.30-1.28	
D (W/L 6-9)	Host	1.29 $\pm$ 0.35	0.35	0.76-2.19	<0.001
	Sex	0.34 $\pm$ 0.11	0.001	0.18-0.55	
	W/L	1.10 $\pm$ 0.26	0.69	0.59-1.75	
	Partial meal	0.60 $\pm$ 0.24	0.19	0.28-1.29	0.012

P(z), significance of odds ratio; P(Wald), model significance; and W/L, weight-to-length ratio.



**Table 3**  
Comparison of the highest probability values for flight initiation of *T. infestans* from all published studies

Study	Experimental setting	Origin of bugs	% flight initiation		W/L	Temp(°C)	Differences between sexes
			Males	Females			
Lehane and Schofield (1981)	Salt flat (Córdoba)	1-yr-old colony	19		ND	23.5	ND
Lehane and Schofield (1982)	Laboratory	10-yr-old colony	5		ND	19	ND
Lehane et al. (1992)	Laboratory	10- and 45-yr-old colonies	22 ± 10 <sup>d</sup>	30 ± 15 <sup>a</sup>	5/6 <sup>b</sup>	24-31	NT
Schofield et al. (1992)	Laboratory	≈10-yr-old colony	5	5	5	25	No
McEwen et al. (1993)	Salt flat (Córdoba)	2-yr-old colony and experimental hut bugs	70	65	5	33	No
This study	Laboratory	≈-yr-old colony	45		5.5/4.5 <sup>b</sup>	29	NT
	Punilla Valley (Córdoba)	2-yr-old colony	35	55	6.5	24-28	NT
		Field collection	57 <sup>d</sup>	76 <sup>d</sup>	<10 <sup>c</sup>	25	Yes
					5/5	25.7 <sup>d</sup>	Yes

ND, no data; NT, not tested.

<sup>a</sup> Mean ± 1 SD (%).

<sup>b</sup> W/L value for males/value for females.

<sup>c</sup> Course estimate based on observation of midgut content and shape.

<sup>d</sup> Average value among series B-D.