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Flight Muscle Dimorphism and Heterogeneity in Flight Initiation of Field-Collected *Triatoma infestans* (Hemiptera: Reduviidae)

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Abstract

Recent experiments demonstrated that most field-collected *Triatoma infestans* (Klug) (Hemiptera: Reduviidae) adults from northern Argentina either never initiated flight or did so repeatedly in both sexes. This pattern could not be explained by sex, adult age, weight, weight-to-length ratio (W/L), or chance. We examined whether bugs that never initiated flight possessed developed flight muscles, and whether flight muscle mass relative to total body mass (FMR) was related to the probability of flight initiation. Approximately half of the adults that never initiated flight had no flight muscles. The absence of flight muscles was 2.4 times more frequent in males than females. Females had significantly larger flight muscle mass than males. For both sexes, the frequency of bugs with no flight muscles was spatially heterogeneous among individual collection sites. A logistic regression model of flight initiation that included both FMR and W/L provided a better fit than models including either one of these predictors. FMR is a novel predictor of flight initiation in Triatominae, with a stronger effect than W/L. The higher frequency of females initiating flight in our experiments may be explained by females having flight muscles more frequently than males, and having FMR and W/L values more suitable for flying. These findings demonstrate that individuals and natural populations of *T. infestans* can differ dramatically with regard to flight initiation.

Keywords

flight muscles; dispersal polymorphism; Triatominae; Chagas disease; reinfestation

Flight dispersal of *Triatoma infestans* (Klug) (Hemiptera: Reduviidae), the main vector of Chagas disease in South America, is probably the most important mechanism of house reinfestation at a village scale following residual insecticide spraying (Schofield 1985, Cecere et al. 2004, Vazquez-Prokopec et al. 2006). Flight initiation of *T. infestans* is associated positively with temperature and negatively with bug nutritional status (estimated by the weight-to-length ratio, W/L); it increases with adult age up to 40–60 d old and then falls to lower constant levels, and it is usually more frequent in females than males (Lehane and Schofield 1982, Williams and Schofield 1985, Lehane et al. 1992, Gurevitz et al. 2006). Additionally, the activity of glycerol-3-phosphate dehydrogenase (GPDH), a major component of energy metabolism, has been found to be higher in flight muscles of fliers than of nonfliers in two other species of Triatominae (Soares and Santoro 2000).

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In recent experiments conducted in experimental huts under natural climatic conditions, most of the field-collected *T. infestans* adults could be divided into those with high probability of repeated flight initiation, and those with very low or zero probability of flying (Gurevitz et al. 2006). Such nonrandom differences could not be explained by sex, adult age, weight, or W/L in a multivariate analysis. Flight polymorphisms have been described in other insect groups (Harrison 1980, Zera and Denno 1997). Typically, these are wing polymorphisms in which one morph lacks fully developed wings and, in some species, this is accompanied by absence of developed flight muscles. In some *Gryllus* species, even some fully winged individuals were found to have no developed flight muscles (Zera et al. 1997). The only case of flight polymorphism reported within Triatominae has been the wing polymorphism in *Mepraia spinolai* Porter, in which males may be macropterous, brachypterous, or micropterous, whereas females are always micropterous (Lent and Wygodzinsky 1979, Schofield et al. 1998). We hypothesized that the *T. infestans* adults that never initiated flight in our experiments might not have developed flight muscles.

Flight muscle ratio (FMR), i.e., the proportion of total body mass represented by flight muscles, is a limiting factor for take-off (flight initiation) in insects, birds, and bats; a minimum FMR of 12–16% is generally needed for take-off (Marden 1987, 2000). We hypothesized that the FMR of *T. infestans* adults that never initiated flight in prior experiments (Gurevitz et al. 2006) might have been too low for take-off. Our aim was to assess whether those bugs had flight muscles and to evaluate the relationship among flight initiation probability, FMR, and W/L, to explain the observed heterogeneity in flight initiation probabilities among individual bugs.

Materials and Methods

Insects

T. infestans bugs used here had previously been used in our flight initiation experiments (Gurevitz et al. 2006). These insects were collected in late summer 2004 from highly infested peridomestic sites (mainly chicken nests in kitchens and store rooms) in four neighboring villages (Kilómetro 34, Kilómetro 40, Invernada Norte, and La Loma) in the Department of Figueroa (27° 23' S, 63° 29' W), Province of Santiago del Estero, Argentina.

Experimental Design

Flight initiation experiments consisted of four experimental series (A–D), each conducted over three to six consecutive nights with repeated measurements of flight initiation on each individually marked bug (Gurevitz et al. 2006). The experiments were carried out in experimental huts within closed cages under natural climatic conditions during late summer 2004. Bugs from series A and B were used 5 and 15 d after being collected in the field as adults, respectively. Bugs from series C were captured as fifth instars in the same sites as the adults, and fed once in the laboratory where they molted, so that adult age was known to within 1 wk. Adults from series C were used 45 d after collection in the field. Bugs from series D had previously been used in series A; they were given a full bloodmeal 15 d after field collection and used again 40 d later. Immediately after completing each experimental series B–D, the body weight and length (from the clypeus to the abdominal tip) of each bug were recorded. Individuals were kept at –70°C until dissection.

The frozen bugs were weighed again and their complete thoracic contents (free of cuticle) were dissected and weighed on an electronic balance (Shimadzu Libror, AEG-220, Duisburg, Germany; precision ± 0.1 mg). The color (red-brown or white) and consistency (firm or liquid) of thoracic contents and the occurrence of dorsolongitudinal and dorsoventral muscles (i.e., flight muscles) were recorded. The data available for 252 males and 154 females were sex;

fresh and frozen body weight; body length; adult age (only for series C); collection site (ecotope and village); flight behavior (whether the bug initiated flight or not on each night of the flight experiments); and flight muscle color, presence, and mass.

For quantifying the specific activity of GPDH in the flight muscles, the thoracic contents were extracted from 24 males and 12 females of series B, randomly chosen from among those bugs that initiated flight every night or never. Thoracic contents were weighed, individually homogenized in 10 mM Tris-1 mM EDTA (TE) buffer, pH 6.6, and centrifuged at 13,000 [time] g for 25 min. The supernatant was separated and 5% (m/v) diluted in the TE buffer. For each individual bug, GPDH activity was spectrophotometrically quantified by following the disappearance of 0.754 mM NADH at 340 nm in the reaction of 0.44 mM dihydroxyacetone into glycerol-3-phosphate at 30°C. Absorbance was recorded every 10 s for 3 min. One unit of enzyme (U) is the amount that uses 1 μ mol of substrate in 1 min of reaction under the assay conditions. The molar extinction coefficient of NADH used was 6.22 liters/mol/cm. Total protein concentration in the supernatant was determined according to Bradford (1976).

Data Analysis

To assess the relationship between flight muscle mass and the observed flight behavior, we used FMR because it is directly related to take-off capacity and is functionally linked to flight capability (Marden 1987). For comparisons of flight muscle mass between sexes and among age classes (only in series C), we used one-way analyses of variance. FMR and the ratio between flight muscle mass and body length also were used for similar comparisons to account for variations in body size among individuals. We used chi-square tests (Zar 1999) to compare the frequencies of flight muscle morphs between sexes, age classes (series C), or collection sites in the field. For comparisons between collection sites, La Loma village was excluded because the few bugs collected there were pooled for convenience.

We used Akaike's information criterion corrected for overdispersed data (QAIC) (Burnham and Anderson 2002) to identify the best-fitting logistic regression model that described flight initiation probabilities (response variable). The candidate models included FMR, W/L, or both as predictors. FMR was considered to be zero for bugs with no flight muscles. For each sex, overdispersion was estimated as the quotient of the goodness-of-fit χ^2 statistic divided by its degrees of freedom for the model with W/L and FMR effects. QAIC differences (Δ_i) were calculated as the QAIC for the i th model minus the minimum QAIC obtained. Model probabilities for the i th model (w_i) (Akaike weights) were calculated as $\exp(-1/2 \Delta_i)$ divided by the sum of $\exp(-1/2 \Delta_i)$ over all models. The Akaike weight of a model is its standardized relative likelihood. These weights can be interpreted as the weight of evidence in favor of model i being the best model for the current situation given that one of the proposed models has to be the best model. The standard errors of the regressions were adjusted for clustering on individual bugs. Because bugs from series B to D had similar flight initiation probabilities, for these analyses they were pooled. In all analyses, the effects of variables other than sex (i.e., W/L, FMR, and adult age) were tested separately for males and females due to their marked differences in flight initiation chances. All analyses were run on STATA 9.0 (Stata Corporation 2005).

Results

In total, significantly more males (21.8%) than females (9.1%) had no flight muscles ($\chi^2=10.4$, $df=1$, $P=0.001$) (Table 1). These bugs presented almost empty thoracic cavities, except for the small (1–9% of total body mass), whitish thoracic contents of almost liquid consistency (Fig. 1A). The rest of the dissected insects exhibited developed flight muscles (9–22% of total body mass) that completely filled up the thoracic cavity, were red-brown, and had a firm consistency (Fig. 1B). Among males, the frequency of flight muscle morphs differed only marginally

between series, with males of series D (the oldest individuals) having no muscles almost twice as frequently as males from series B or C. Adult age within 2–5 wk postemergence was not significantly associated with the absence of flight muscles in either sex (Table 2). None of the bugs with no flight muscles had been recorded as fliers in previous experiments. Of the 104 (41%) males and 29 (19%) females that never initiated flight, 53 and 48% had no flight muscles, respectively. Among bugs with flight muscles, 25% (49/197) of males and 11% (15/140) of females never initiated flight; on average, 56% of males and 74% of females initiated flight each night of the experiments.

Among those *T. infestans* with flight muscles, females had significantly larger flight muscle mass than males ($F = 52.3$; $df = 1, 135$; $P < 0.001$). This relationship also held for FMR ($F = 156$; $df = 1, 335$; $P < 0.001$) and for the ratio between flight muscle mass and body length ($F = 22.8$; $df = 1, 335$; $P < 0.001$). In series C, flight muscle mass showed no significant differences among age classes in males ($F = 1.43$; $df = 3, 71$; $P = 0.24$) or females ($F = 1.43$; $df = 3, 56$; $P = 0.24$). Similarly, flight muscle mass relative to body length did not differ significantly among age classes for males ($F = 1.73$; $df = 3, 71$; $P = 0.17$) or females ($F = 1.40$; $df = 3, 56$; $P = 0.25$). In both sexes, FMR differed significantly according to the number of nights that each bug with flight muscles initiated flight (males: $F = 5.90$; $df = 3, 193$; $P < 0.001$; and females: $F = 4.74$; $df = 3, 136$; $P = 0.004$) (Fig. 2). These differences arose from the lower FMR mean of the nonflier group. The observed minimum FMR value for a flier was 11.7% for males and 13.5% for females; only six males and two females with flight muscles were below the minimum FMR values for fliers.

For all dissected males and females, a logistic regression model that included both FMR and W/L provided a better fit than models including either of them according to QAIC (Table 3). Addition of the interaction between FMR and W/L did not improve the fit of the model (data not shown). FMR alone performed better than W/L alone, although in males not much support was found for either model. For both sexes, FMR had a positive effect on flight initiation probability whereas W/L had a negative effect (Table 4). The odds ratios for each variable were almost equal between sexes. Very similar results were obtained when only bugs with flight muscles were included in the analysis (data not shown). After excluding bugs that were below the observed minimum FMR value for a flier (i.e., 11.7% for males and 13.5% for females), a much weaker contribution of FMR to model fit was obtained (data not shown).

The frequency of bugs with no flight muscles collected from individual sites significantly departed from homogeneity among sites for both males ($\chi^2 = 45.7$, $df = 9$, $P < 0.001$) and females ($\chi^2 = 42.7$, $df = 9$, $P < 0.001$). The frequency of bugs with no flight muscles was markedly higher in one pig corral for both sexes, and only for males in several sites in La Loma village that were pooled (Fig. 3).

Among bugs with flight muscles, GPDH mean activity was lower in nonfliers (males: $N = 3$, mean \pm SE = 0.07 ± 0.05 U/mg protein; females: $N = 10$, mean \pm SE = 0.06 ± 0.04 U/mg protein) than in fliers (males: $N = 9$, mean = 0.111 ± 0.05 U/mg protein; females: $N = 10$, mean = 0.09 ± 0.05 U/mg protein). Differences between these small samples were not statistically significant (males: $F = 2.73$; $df = 1, 18$; $P = 0.12$; and females: $F = 0.77$; $df = 1, 10$; $P = 0.40$).

Discussion

Our study yielded four main results: 1) field-collected *T. infestans* adults were dimorphic for flight muscles. Approximately one-half of the adults that never initiated flight did not have the flight muscles to do so, and the absence of flight muscles was 2.4 times more frequent in males; 2) FMR was a stronger predictor than W/L and considerably improved the fitting of the flight initiation model over models that only included FMR or W/L; 3) variations in FMR and W/L

jointly explained the observed higher flight initiation probabilities of females than males, and 4) the frequency of bugs with no flight muscles was spatially heterogeneous for both sexes.

The absence of developed flight muscles in insects may be the result of degeneration of developed muscles, arrested growth of muscles, or both (Zera and Denno 1997, Marden 2000). Although our study design did not allow us to distinguish between these alternatives, the 1.7–4.1-fold increase in the frequency of bugs with no flight muscles in series D with respect to series B suggests that some of the former bugs (which on average were 1.5 mo older and had spent this period in the laboratory) might have undergone an age- or condition-related degeneration of developed flight muscles. The absence of a clear trend with age in morph frequencies within the first 2–5 wk as adults in series C suggests that muscle degeneration may occur beyond this time period.

In insects, flight muscle dimorphism is due to genetic variance (as in some beetles), to environmental variance (as in aphids), or most frequently, to both, as in waterstriders, planthoppers, and crickets (Zera and Denno 1997, Zera 2004). For *T. infestans*, possible environmental factors may include stability and availability of resources (mainly, hosts and mates), frequency of insecticide spraying (or other cases of population bottlenecks or recolonizations), and age of the colony. Some of these variables also may determine the adaptive value of dispersal. Environmental factors that can affect flight initiation probabilities do not necessarily act during or just before the flying event, but they may have operated several months beforehand. For example, an increase in feeding frequency during the fifth instar of *T. infestans* was associated with faster development of males, increased size of females and decreased flight initiation probability in both sexes (McEwen and Lehane 1993). The relative contribution of genetic and environmental variance to the observed flight muscle dimorphism may have important ecological and evolutionary consequences.

Wing polymorphism in insects is associated with variation in a variety of biochemical, physiological, and behavioral traits (Zera and Denno 1997, Zera and Harshman 2001). Of particular importance is the negative association between presence of wings and ovarian mass (and thus, female fecundity), as found in some Orthoptera and Hemiptera. Moreover, it is not the presence of wings per se, but rather the maintenance of flight muscles that generates the trade-off between fecundity and dispersal capability in some *Gryllus* species (Zera et al. 1998, Zhao and Zera 2002). In Triatominae, Oliveira et al. (2006) reported an interruption in lipid flow to ovaries during flight of *Rhodnius prolixus* Stål. and a severe decrease in egg production after daily exhaustive flights. Altogether, this suggests that *T. infestans* females with no flight muscles may have higher fecundity than those with flight muscles. If the heterogeneity in morph frequencies observed among individual collection sites is accompanied by differences in female fecundity, the reproductive output of bug populations also would be heterogeneous under similar conditions and availability of resources among sites.

Our study identified FMR as a novel predictor of flight initiation, with a stronger effect than W/L. Consideration of the presence of flight muscles jointly with FMR and W/L in a logistic regression model provided a better description of flight initiation probabilities under our experimental conditions than did previous models (Lehane et al. 1992, Gurevitz et al. 2006). In the best-fitting model, flight initiation probabilities for both sexes were modified by the same variables and in a quantitatively similar manner. Thus, the higher frequency of females initiating flight in our experiments may be because they had flight muscles more frequently than males, and FMR and W/L values (or some other factor intimately related to them) more suitable for flight initiation. The absence of flight muscles also may explain why a significant fraction ($\approx 50\%$) of experimental *T. infestans* adults with low W/L ratios (< 6 mg/mm), and consequently high predicted chances of flying, did not fly at all in spite of adequate environmental conditions (Schofield et al. 1992). The effects of increasing FMR above the

putative threshold may translate into longer flight times and consequently into a larger flight range. The larger flight muscle mass exhibited by females (both in absolute and relative terms) would imply a higher capacity than males to carry extra load (such as eggs or more energy reserves for sustained flight) as well as longer flights and a broader flight range. This set of attributes in female *T. infestans* underscores the role that flight dispersal may play in reinfestation after insecticide sprays at a village scale and contrasts with the major role attributed to passive transport by humans as a major driver of local reinfestation in disregard of flight dispersal (WHO 2002).

In a wide spectrum of insect and vertebrate species, the minimum FMR that allows take-off ranges from 12 to 16% (Marden 1987, 2000). Similarly, in our study no bug with $FMR < 11.7\%$ initiated flight, but only seven insects had both flight muscles and $FMR < 11.7\%$. This suggests that among bugs with flight muscles, FMR did not limit flight initiation severely. The large number of bugs that initiated flight with FMR values close to 12% (males) and 14% (females) suggests that the FMR threshold for *T. infestans* would be below these values. However, current FMR values are not accurate because they were based on the muscle mass of frozen insects that may have lost some mass due to dehydration. The higher flight muscle GPDH activity observed in fliers compared with nonfliers is consistent with the pattern found in *Panstrongylus megistus* (Burmeister) and *Triatoma sordida* Stål (Soares and Santoro 2000) and suggests that GPDH activity may be similarly associated with flight behavior in *T. infestans*.

The current findings demonstrate the necessity of assessing the FMR to have precise estimates of flight initiation probabilities of *T. infestans*. In addition, this study demonstrates that individuals and natural populations of *T. infestans* can differ dramatically with regard to a fundamental trait such as flight dispersal. Such heterogeneity within and between natural populations of *T. infestans* may be relevant to reinfestation dynamics and gene flow after control actions.

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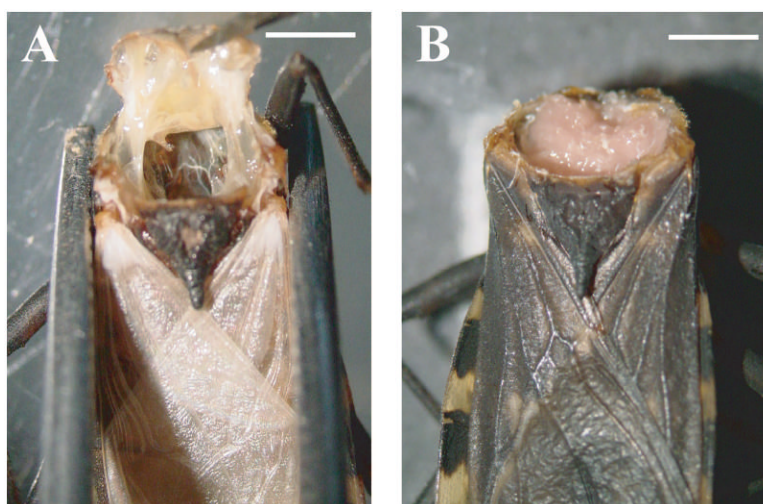
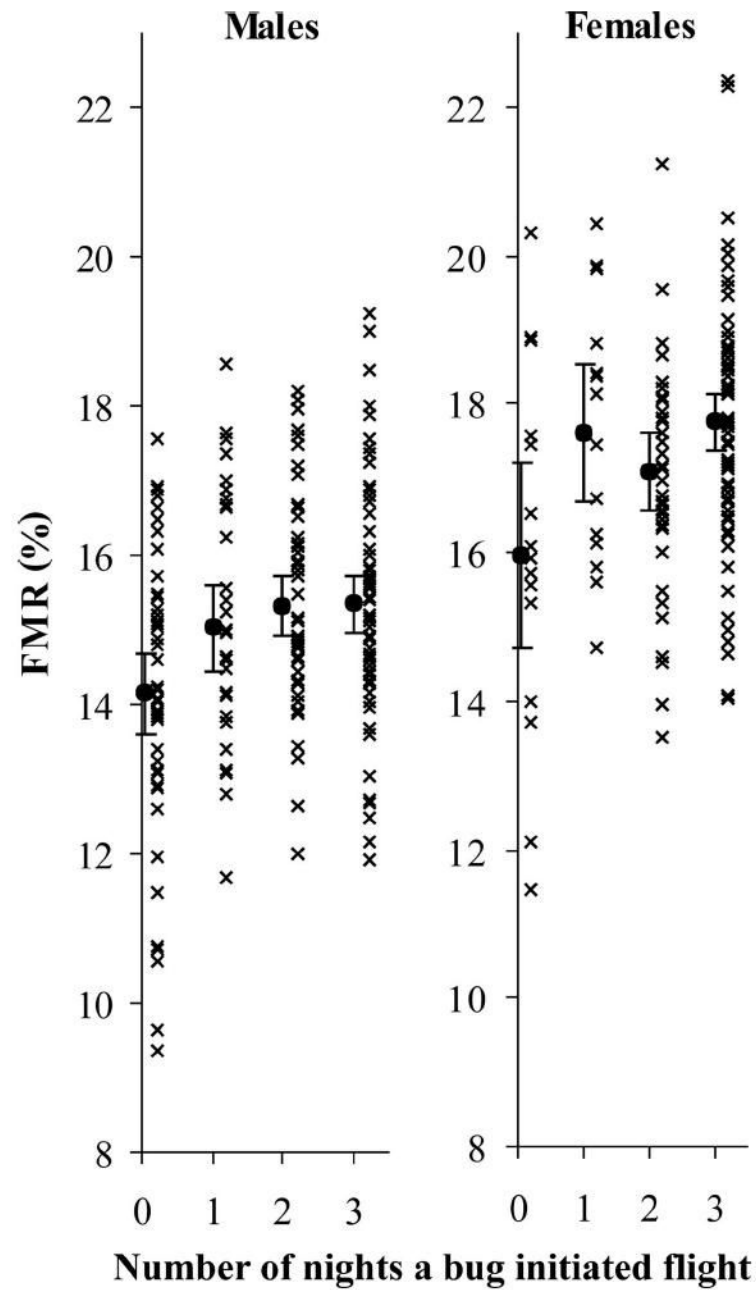
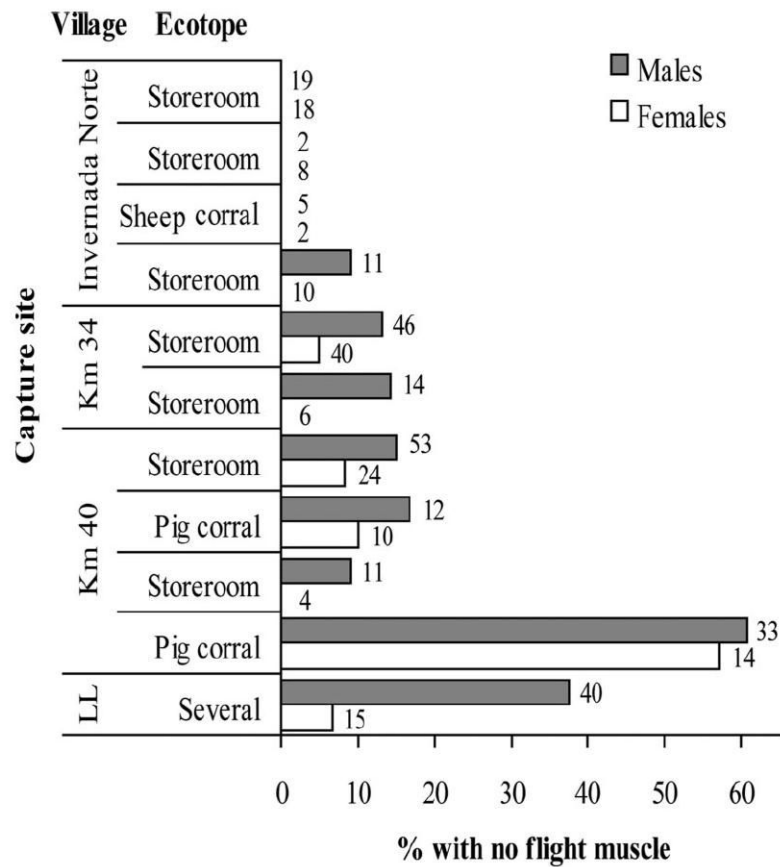


Fig. 1. Macroscopic appearance of the thoracic contents of a *T. infestans* adult (A) with no flight muscles and (B) with flight muscles. Scale bar = 3 mm.

**Fig. 2.**

Sex-specific FMR of *T. infestans* with flight muscles according to number of nights that each bug initiated flight. Black circles and lines show the mean FMR and its 95% CI, respectively. Crosses indicate individual FMR values for each bug. Bugs from the three series (B–D) are pooled.

**Fig. 3.**

Frequency of *T. infestans* adults with no flight muscles in each collection site in northern Argentina. The village and ecotope of each site is specified. The number of bugs of each sex collected in each site and dissected is indicated beside each bar. Bugs from the three series (B–D) are pooled. LL, La Loma village.

Table 1

Frequency of *T. infestans* males and females with no flight muscles in each of the three (B–D) experimental series of flight initiation

Series	% bugs with no flight muscles (no. of bugs dissected)	
	Males ^a	Females ^b
B ^c	18.3 (82)	2.6 (39)
C ^d	16.7 (90)	11.8 (68)
D ^c	31.3 (80)	10.6 (47)
Total	21.8 (252)	9.1 (154)

The chi-square tests between sexes within each series and among series within each sex are indicated.

^a df = 2, $P < 0.05$.

^b df = 2, $P > 0.25$.

^c df = 1, $P < 0.02$.

^d df = 1, $P = 0.4$.

Table 2Frequency of *T. infestans* males and females with no flight muscles according to adult age for series C

Adult age (wk)	% bugs with no flight muscles (no. of bugs dissected)	
	Males ^a	Females ^b
2	23.5 (17)	0 (6)
3	12.6 (40)	16.0 (25)
4	35.7 (14)	5.3 (19)
5	5.3 (19)	16.7 (18)
Total	16.7 (90)	11.8 (68)

The chi-square test among age classes within each sex is indicated.

^a df = 3, $P = 0.1$.

^b df = 3, $P > 0.5$.

Table 3
Summary of Akaike's information criterion corrected for overdispersed data (QAIC) and associated statistics for logistic regression models of the effects of W/L and/or FMR on flight initiation probability of all field-collected *T. infestans* that were dissected

Model	<i>k</i>	Males			Females		
		QAIC	Δ_i	w_i	QAIC	Δ_i	w_i
W/L FMR	3	462.863	0.00	0.94	263.898	0.00	0.66
FMR	2	468.407	5.54	0.06	265.195	1.30	0.34
W/L	2	604.653	141.79	0.00	324.212	60.31	0.00

Series B–D were pooled. *k*, number of model parameters estimated; Δ_i , QAIC differences; and w_i , model probabilities (Akaike weights).

Table 4

Logistic regression analyses of W/L and FMR on flight initiation probability of all field-collected *T. infestans* that were dissected

Sex	Independent Variable	Odds ratio \pm SE	95% CI
Male	W/L	0.78 \pm 0.08	0.64–0.94
	FMR	1.37 \pm 0.04	1.29–1.46
Female	W/L	0.81 \pm 0.08	0.66–0.99
	FMR	1.34 \pm 0.07	1.21–1.47

Series B–D were pooled. SE values were adjusted for clustering on individual bugs. CI, confidence interval.