



Female choosiness and mating opportunities in the blood-sucking bug *Rhodnius prolixus*

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Abstract

We investigated the relationship between female choosiness and mating opportunities in the blood sucking bug *Rhodnius prolixus*. *Rhodnius prolixus* females exhibit active discrimination behaviour to male mating attempts which delays or prevents copulation. Female rejection behaviours can be beneficial if mating opportunities are readily available and the pool of males varies in their quality. Thus, the benefits of finding a better quality male may override the cost of rejecting a mating opportunity. Since the availability of mating opportunities is affected by the ratio of sexually active males to females, we randomly assigned focal pairs to arenas with a sex ratio biased toward males, females or without other individuals. More females exhibited rejection behaviour when conspecifics were present, however, no differences were found when the sex ratio was biased toward either males or females. We discuss possible explanations for these results and hypothesize about the adaptive function of female rejection behaviour.

Keywords

female choice, rejection behaviour, female discrimination, mating.

1. Introduction

Female mate preference plays a crucial role in the evolutionary process (Cronin, 1991). A considerable body of scientific evidence shows that females have strong preferences for mating with high quality males in species

in which the female invests more in the germ cells than the male does. By mating with high quality males, the female ensures that its past and future energy input in the egg, and the raising of the progeny, maximizes her fitness (Trivers, 1972). High quality males may provide resources or genetic benefits (Vahed, 1998) and usually have distinctive traits which differentially attract females (Whitney & Krebs, 1975).

A choosy female faces two general tasks in selecting a male. First, she must either attract or actively search for males. Once she encounters one or more males, she must then decide whether to accept or reject them as mates (Dugatkin & Godin, 1998). Several studies have highlighted variability in female mate choice (Kodric-Brown & Nicoletto, 1996). Female choice are influenced by factors such as female parasite load (Poulin, 1994; López, 1999; Pfennig & Tinsley, 2002), female age (Kodric-Brown & Nicoletto, 2001; Moore & Moore, 2001; Coleman et al., 2004; Uetz & Norton, 2007) and female experience (Collins, 1995; Hebets, 2003; Hebets & Vink, 2007). Environmental or ecological factors such as predation risk or seasonal changes may also affect female mating decisions (Hedrick & Dill, 1993; Borg et al., 2006).

Variation in female choice could be due to variability in preferences, degree of choosiness, or both. While ‘preferences’ reflect the order in which an individual ranks prospective mates *ceteris paribus*; ‘choosiness’ refers to the effort or energy that an individual invest in assessing mates (Jennions & Petrie, 1997). The degree of female choosiness has strong implications for evolution by sexual selection. Increased choosiness — by changes in sampling tactics or a higher mating threshold — may intensify the strength of sexual selection.

Choosier females are selected when potential mates are both abundant and variable in quality (Bleu et al., 2012). Under such circumstances the benefits of finding a better quality male may override the benefits of mating with the current male. The availability of mating opportunities is affected by the ratio of males to females that are sexually active (referred to as the operational sex ratio (OSR); Emlen & Oring, 1977). The greater the imbalance in the OSR, the greater the sexual competition among members of the limited sex (Emlen, 1976). Thus, the benefits and costs of choosiness may vary with the range in quality of potential mates. We have not found any empirical evidence showing whether the availability of sexual partners affects female choosiness. On this basis, we study the blood-sucking bug *Rhodnius*

prolixus (Hemiptera: Reduviidae: Triatominae) to determine whether female choosiness is influenced by the presence of potential mates (males) and sexual competitors (females).

Rhodnius prolixus is a convenient insect model for the study of female choosiness because females exhibit active discrimination behaviour in response to male copulatory attempts. Previous works in several triatomine species show that females actively reject potential partners through the display of behavioural stereotypes, such as flattening close to the substrate, stridulation, evasion (running away) and abdominal movements (Manrique & Lazzari, 1994; Pires et al., 2004; Vitta & Lorenzo, 2009). These behavioural stereotypes may prevent the physical contact with the male or limit his access to the female's genitalia. We identify here the behavioural stereotypes related to rejection behaviour in *R. prolixus*.

In order to study whether female choosiness is affected by the availability of mating opportunities, mating pairs were placed in an experimental arena in which they were exposed to either (i) three additional conspecific males (male-biased sex ratio), (ii) three additional conspecific females (female-biased sex ratio) or (iii) no additional conspecifics (control group). The expectation is that female choosiness may vary according to its cost. Thus, when the ratio between females and males is biased toward males the frequency of female rejection behaviour will be higher since the costs of rejecting a mating opportunity are low (there are more males potentially available), and females can increase their reproductive success by choosing a male with potentially better qualities. On the other hand, when the ratio between females and males is biased toward females rejection will be less frequent since the cost of losing a mating opportunity is high and the possibility of choosing among males of different qualities does not exist.

2. Materials and methods

2.1. Insects

R. prolixus used in our study were reared in our laboratory insectary from eggs at $28 \pm 1^\circ\text{C}$ temperature and 30–60% relative humidity, under a 12:12 h (L:D) illumination regime. All instars were fed weekly ad libitum for about 45 min on live hens. During the feeding session, the bugs were kept inside a cylindrical acrylic flask (9.5 cm high \times 8.5 cm diameter) with a piece of filter paper as substrate and a nylon mesh as a cover and a floor. Each flask

was gently placed in close contact to the hen's skin and therefore insects used the substrate to walk and reach the food source.

Insects were sorted by sex after the imaginal ecdysis, keeping each sex segregated in different plastic containers until the experiments were performed. We used virgin adults that were between 7–35 days old. The difference between the youngest and the oldest experimental individual corresponds to about 8% of the maximum lifespan. The experimental subjects were starved for 5–21 days postecdysis prior to the experiments. The maximum duration of starvation used here does not affect the normal activities of *Rhodnius*, which have a strong resistance to longer periods of starvation (Cabello, 2001). Although the potential influence of age and starvation period is not correlated with treatments they will be included in the statistical analysis.

Insects were used only once and then discarded. All experiments were carried out during the first hours of their scotophase so to match the maximal activity period observed for triatomines (Lazzari, 1992). Experiments were performed at a homogeneous illumination intensity of 15 lux, enough to both allow the experimenter to observe the bugs and avoid insect disturbance by high illumination intensity. The temperature of the experimental room was set to $25 \pm 2^\circ\text{C}$ before the beginning of each assay with an electric fan heater, which was turned off before starting each experiment. The relative humidity ranged between 44 and 50%.

We did not observe any harmful effects associated to our experimental manipulation. At the end of the experiment the insects were returned to their breeding cages and the hens to the chicken coop. All animals were handled according to the biosafety rules from the Servicio de Higiene y Seguridad of the Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina.

2.2. *Experimental device*

The female behaviour displayed under the different experimental sex ratios was tested using an experimental arena that consisted of a circular acrylic box (2.5 cm height \times 14 cm diam.) divided in two equal parts by an odour-permeable removable acrylic partition (14.3 \times 2.5 \times 0.8 cm) which had three lines of 10 holes (0.4 cm diam.) each one spaced by 2 cm comprising a total of 30 holes. Each hole was vertically spaced from the adjacent one by 0.3 cm. Another odour-permeable removable acrylic minor partition, with a

total of 15 holes aligned in the same manner as previous, divided one half of the arena in two equal parts. Thus, three compartments were defined. Three elliptical entrances (2×1.5 cm diam.) on the lateral side of the arena (one centred at one half and the other two at both halves) allowed the release of insects into the arena. The box and the elliptical entrances were covered by removable lids after releasing the insects. A filter paper matching the floor of the arena served as substrate to avoid possible chemical contamination between assays, as it was changed every time new bugs were released.

2.3. Treatment groups

The experimental arena allowed to measure female rejection behaviours in presence/absence of more individuals. Female *R. prolixus* were randomly exposed to three treatment groups: sex ratio biased toward females (F+), sex ratio biased toward males (M+) and absence of additional individuals (A).

In all treatments a focal pair was placed in one half of the arena. The additional individuals were placed in the other half. In F+, the additional individuals were three females ($N = 25$). In M+, three males ($N = 27$), and in A no additional individuals were present ($N = 28$) (Figure 1).

2.4. Procedure

In each assay, the insects were individually released into one compartment of the arena, with the two smaller compartments randomly assigned to the focal male or female and the third larger one to the three stimulus individuals in the case of the F+ and M+ treatments. The three stimulus individuals were released first, then the focal female, and finally the focal male. To avoid mechanical disturbance that could trigger a discharge of Brindley's and metasternal glands when released into the arena, each individual was allowed to climb onto a piece of filter paper, which was then placed into each compartment, letting the insects walk freely (Manrique et al., 2006). After 5 min of familiarization to the arena, the minor partition was removed, allowing focal female-male interactions. The observation and monitoring of behaviour lasted until the first copulation or until 60 min elapsed (i.e., no copulation). This time was selected by taking into account that copulation in *R. prolixus* lasts about 50 min. The insect's behaviour was recorded using a video camera (Cctv Ccd 420 tvl, Monitor, China) placed 30 cm above the arena and connected to a digital recorder (4CH-H.264 DVR, China). After each assay the insects were carefully removed from the arena with a piece

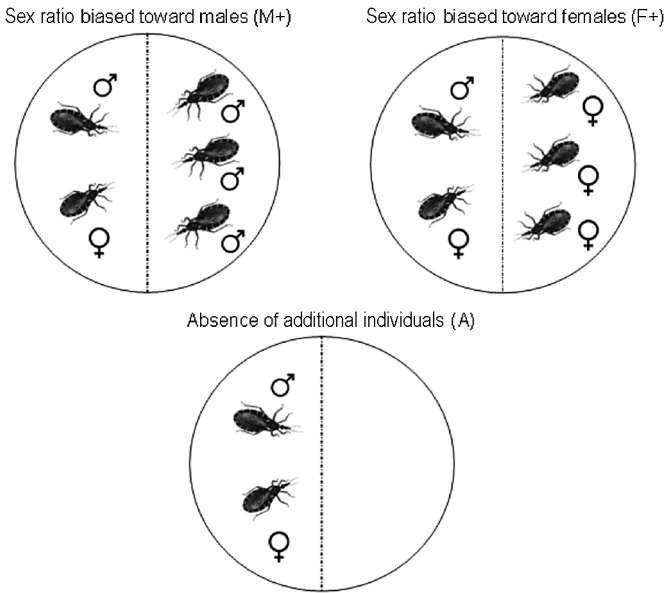


Figure 1. Diagram of the experimental set up. Insects were tested in circular acrylic arenas, separated by a transparent odour-permeable barrier full of holes. Focal couples were randomly exposed to three treatment groups: F+, with a sex ratio biased toward females; M+, with a sex ratio biased toward males; A, in absence of additional individuals.

of filter paper to avoid disturbance and the focal individuals were weighted and their thorax lengths measured. The focal female remained isolated into a flask in order to look for the presence of a spermatophore in the two subsequent days, an indicator that copulation had indeed occurred.

2.5. Statistical analyses

As a first approach to our data, regardless of treatments, we described and quantified the eventual occurrence of stereotyped behaviours exhibited by the female in presence of the male. In order to identify which stereotyped behaviours exhibited by *R. prolixus* females were associated with the absence of copulation we performed a correspondence analysis (CA). We analysed the relationship between female rejection behaviour and copulation using a logistic regression, with 'rejection behaviour' (Yes/No) as the explanatory variable and 'copulation' (Yes/No) as the dependent variable. 'Age' (average of intervals) and 'starvation period' (measured as days of food deprivation prior to the experiment) were included in the model as covariates.

The effects of sex ratio on female rejection behaviour was analysed using a logistic regression, in which the explanatory variable was ‘treatments’ (F+, M+) and the dependent variable was ‘rejection behaviour’ (Yes/No). We performed the regression using ‘age’ and ‘starvation period’ as covariates.

We recorded additional information such as female weight, male weight and male thorax length in a sub-sample of individuals. Their potential relationship with rejection behaviour was analysed separately to avoid a reduction in the number of observations.

We fitted all models in STATA (Data Analysis and Statistical Software, StataCorp LP).

3. Results

3.1. Identification of behavioural stereotypes

Mating in *R. prolixus* is typically initiated by a jump or mounting of the male on the female. Then the male tilts laterally and grasps the female dorsally and ventrally using his three pairs of legs to allow the approximation of its genitalia. Once the male reach this position his genitalia join the female genitalia and copula occurs, lasting about 50 min. As a response to male’s copulatory attempts females exhibited six kinds of behavioural stereotypes: (a) abdominal movements: the female shakes her legs and body up and down. These movements difficult the lateral positioning of the male; (b) flattening: the female pushes her body against the substrate, impeding the correct positioning of the male’s legs; (c) evasion: the female runs away once the male jump or mount her, avoiding his physical contact; (d) stridulation: once in contact with the male the female rubs the end of her rostrum against the prosternal groove. The stridulatory vibrations migrate from the female to male’s body and then he stops the copulatory attempt (as already observed in Manrique & Schilman, 2000); (e) stamping: the female responds to the male mounting by bringing their legs down forcibly on the ground, impeding the male stability; (f) abdominal raising: once the male mounts the female she elevates and keeps the abdomen up, avoiding contact of the genitalia.

It is worth noting that these different behavioural stereotypes do not follow a sequential order.

The most frequent stereotyped behaviour observed was evasion, exhibited by 73.68% of females, followed by stamping (47.36%), abdominal raising (27.78%), stridulation (22.22%), and finally abdominal movements and flattening (both 11.11%).

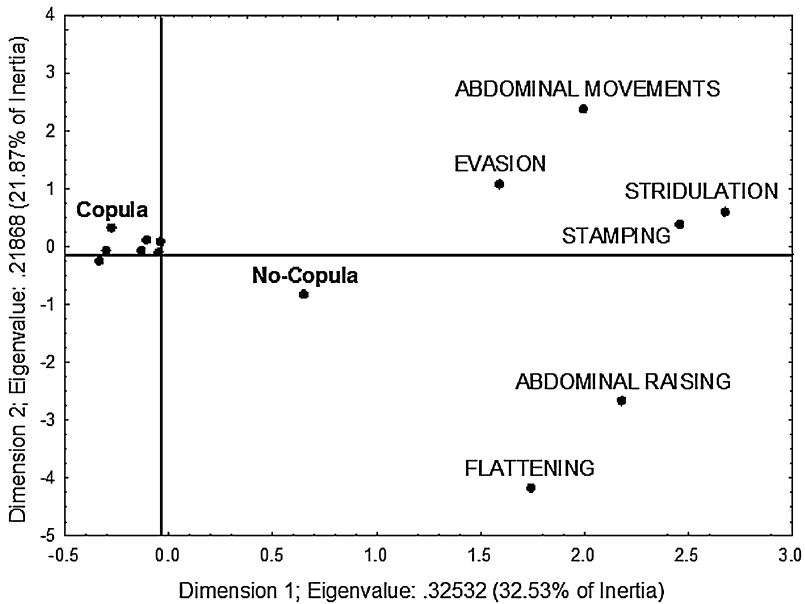


Figure 2. Correspondence analysis showing that the six behavioural stereotypes observed (evasion, abdominal movements, stamping, stridulation, abdominal raising and flattening) are associated with the absence of copula (No-Copula). Analysis explained 54.4% of the variability in dimensions 1 and 2. Percentage of inertia explained by dimension 1 and 2 is given in parentheses.

3.2. Relationship between behavioural stereotypes and rejection

A correspondence analysis (CA) indicated that the six behavioural stereotypes identified were associated with the absence of copula (Figure 2). The absence of copula (No-Copula) and all behavioural stereotypes were mostly and positively represented by dimension 1.

In the absence of stereotypes most of encounters (77%) ended up in copula. On the other hand, when females exhibited stereotypes the frequency of copula was 47.4%. The results of a logistic regression, with 'rejection behaviour' (Yes/No) as explanatory variable and 'copulation' (Yes/No) as dependent variable showed that the exhibition of rejection behaviour is associated with a significant decrement in the occurrence of copula of around 30 percentage points (Table 1). Differences in age and the starvation period of the individuals (included in the model as covariates) did not affect the results ($p > 0.10$).

Table 1.
Copula and rejection.

	Copula	
	Analysis without covariates	Analysis including covariates
Rejection	−0.2968* (0.1266)	−0.2957* (0.1268)
Age		0.0048 (0.0325)
Starvation period		−0.0055 (0.0365)
Number of observations	80	80

Standard errors are shown in parentheses. All models are estimated using a logistic model-logit. Marginal effects evaluated at the means of the independent variables are reported. *Significant at the 5% level.

In addition, the latency to copula was marginally longer when females displayed at least one stereotype (t -test: $t_{54} = 1.94$, $p = 0.057$).

Copula occurrence did not significantly differ between females that performed only one type versus those that displayed different kinds of rejection behaviours (one-tailed Mann–Whitney U -test: $U = 43$, $N_1 = 9$, $N_2 = 10$, $p = 0.43$). However, copula occurrence marginally decreased when females increased the number of rejection behaviours performed (one-tailed Mann–Whitney U -test: $U = 28$, $N_1 = 9$, $N_2 = 10$, $p = 0.06$).

Taken together, these results support the hypothesis that behavioural stereotypes play the role of rejecting copulatory attempts. From now on behavioural stereotypes will be considered as rejection behaviours.

3.3. Individuals' traits and rejection

From the sub-sample of individuals in which additional measures were recorded, we found that a female's weight is related to the incidence of rejection behaviour: females which did not exhibit rejection behaviour were heavier than females which exhibited rejection behaviour (t -test: $t_{71} = -3$, $p = 0.004$). Female weight did not vary significantly among treatments, as expected due to the random assignation of females to each treatment (one-way ANOVA: $F_{2,72} = 0.99$, $p = 0.38$).

On the other hand, male weight and body length did not affect the exhibition of female rejection behaviour (t -test: $t_{72} = 0.21$, $p = 0.83$ and one-tailed Mann–Whitney U -test: $U = 490.5$, $N_1 = 18$, $N_2 = 55$, $p = 0.95$, respectively).

Neither the kind of copula attempt (jump or mounting) nor the latency to copula attempt affected female rejection incidence (Chi-square test: $\chi_1^2 = 0.029$, $p = 0.86$ and one-tailed Mann–Whitney U -test: $U = 437.5$, $N_1 = 19$, $N_2 = 61$, $p = 0.11$, respectively).

3.4. Effects of competition

The results of a logistic regression, with ‘treatments’ (F+/M+) as explanatory variable and ‘rejection behaviour’ (Yes/No) as dependent variable showed that the presence of additional individuals significantly increased the occurrence of rejection behaviours in around 35 percentage points ($p \leq 0.01$). The test that the coefficients on M+ and F+ are equal could not be rejected ($p = 0.92$), meaning that the increment in the occurrence of rejection behaviours was similar both under M+ and F+ treatments (Table 2 and Figure 3). Neither starvation period nor age (included in the model as covariates) affected female rejection behaviour ($p > 0.10$). Moreover, the results of the test of orthogonality show that neither age nor starvation period are correlated with treatments ($p > 0.10$), as expected due to the random assignation of the experimental subjects to each treatment.

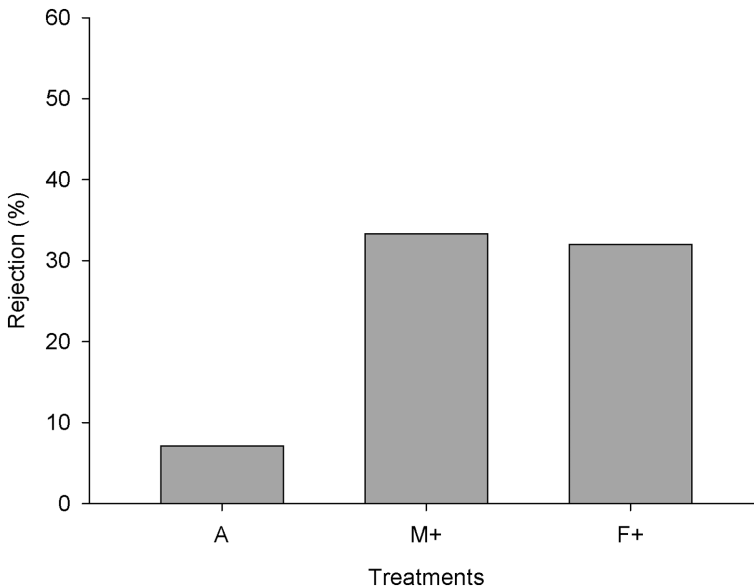


Figure 3. Percentage of females performing rejection behaviours among different treatments: sex ratio biased toward females (F+), sex ratio biased toward males (M+) and absence of additional individuals (A).

Table 2.

Treatments and female rejection.

	Rejection	
	Analysis without covariates	Analysis including covariates
M+	0.3489* (0.1511)	0.3495* (0.1513)
F+	0.3431* (0.1584)	0.3622* (0.1618)
Age		−0.0172 (0.0276)
Starvation period		0.0160 (0.0307)
Number of observations	80	80

Standard errors are shown in parentheses. All models are estimated using a logistic model-logit. Marginal effects evaluated at the means of the independent variables are reported. The hypothesis that the coefficients on M+ and F+ are equal cannot be rejected; $p = 0.92$. *Significant at the 5% level.

The variety (number of types of rejection behaviour exhibited) and intensity of rejection behaviours (frequency in which a rejection behaviour is exhibited regardless its kind) did not change among treatments F+ and M+ (t -test: $t_{15} = -0.28$, $p = 0.78$ and $t_{15} = -0.4$, $p = 0.69$, respectively).

The treatments did not affect the effectiveness of rejection behaviours to prevent copula (Chi-square test: $\chi^2_2 = 0.014$, $p = 0.99$) nor the latency to the first mating attempt to copula (One-way ANOVA: $F_{2,56} = 0.24$, $p = 0.78$).

Treatments did not affect the number of copula attempts (one-way ANOVA: $F_{2,79} = 0.76$, $p = 0.47$), nor the duration of both copula (Kruskal–Wallis test: $H_2 = 4$, $p = 0.13$) and post copula (one-way ANOVA: $F_{2,56} = 0.72$, $p = 0.49$).

4. Discussion

We investigated whether the availability of potential mating opportunities affects female choosiness in the blood-sucking bug *R. prolixus*.

To that end, we first identified in this species the stereotypical behaviours exhibited by females that can be considered as sexual rejection. We found that *R. prolixus* females perform six kinds of rejection behaviour which delays or prevents copulation. Besides stridulation (observed under mating context in *R. prolixus* females; Manrique & Schilman, 2000), we identified: abdominal movements (shaking its legs and body up and down), flattening (pushing the ventral part of its body against the substrate), evasion (running

away), stamping (bringing its legs down forcibly on the ground) and abdominal raising (elevating and keeping the abdomen up). Abdominal movements, flattening, evasion and/or stridulation in response to male copulatory attempts have been observed in other triatomines (Manrique & Lazzari, 1994; Roces & Manrique, 1996; Pires et al., 2004; Lazzari et al., 2006; Vitta & Lorenzo, 2009), whereas stamping and abdominal raising have not yet been described in other triatomine species and could be specific to *R. prolixus*. We show that exhibiting at least one of these rejection behaviours is associated with a significant decrease in the likelihood of copulation. Copulation frequency did not significantly differ between females that perform a unique type versus those that display different kinds of stereotyped behaviours. However, copula occurrence marginally decreased when females increased the number of stereotyped behaviours performed (regardless its kind). Thus, effectiveness would rely on persistence rather than on variety.

We analysed whether the availability of potential mating opportunities (manipulated through changes in the sex ratio) affects female choosiness (measured as the frequency in which females reject a courting male). We found that females exposed to additional individuals significantly reject males more than females exposed to a solitary male. In contrast to our prediction, females responded similarly when the sex ratio was male-biased as when it was female-biased. Notice that both the male-biased and female-biased treatments involve increasing the number of conspecifics in the mating trials. As most triatomines, *R. prolixus* lives aggregated inside their refuges. This might indicate high population density. Perhaps, under such circumstances, opportunities for copulation can be assessed based on number of individuals that are present, regardless of whether they are females or males. Another possibility is that the experimental barrier allowed females to identify the presence of conspecifics but did not allow them to distinguish between females and males. We consider this possibility unlikely since the barrier was transparent and had plenty of holes for odor circulation, which would permit access to visual and olfactory cues.

The fact that neither olfactory nor visual cues allowed focal females to distinguish between a sex ratio biased toward females or males suggests that another cue not present here plays such a role in nature. For example, tactile cues (which were not possible in our experiment) might be important in nature. In fact, *R. prolixus* males and females seem to differ in the proportion of

some cuticular compounds (A.N. Lorenzo Figueiras, personal communication). Thus, contact chemoreception may play a crucial role in distinguishing a conspecific's sex.

We hypothesized that female rejection evolved in a competitive scenario in which the payoff of getting a male with higher qualities overrides the cost of rejecting a mating opportunity. Thus, female rejection behaviour should be dependent on the quality of a male's traits. We tested this hypothesis by comparing ex post phenotypic traits related to size (such as thorax length and weight) of the males assigned randomly to each treatment. We also assessed whether males differed behaviourally with respect to the time in which they made their first attempt to copulate and the type of copula attempt (sometimes they jump from a short distance and other times they mount the female by climbing slowly onto her). Against our expectation, female rejection was not related to male size or behaviour.

We also explored the possibility that rejection behaviour is related to female age. Previous studies found that older female guppies are less choosy than young ones, and virgins are less choosy than non-virgins (Kodric-Brown & Nicoletto, 2001). Likewise, Moore & Moore (2001) show that reproductive aging caused by delayed mating resulted in reduced choosiness by female cockroaches *Nauphoeta cinerea*. Our expectation is that young virgin females may be choosier than mature virgin females since the cost of waiting for higher-quality males is lower than for mature females, which are relatively closer to death and at a higher risk of ovipositing unfertile eggs. Since females with different ages (range: 7 to 35 days) were randomly assigned to each treatment we analysed this possibility ex post. We could not find however empirical evidence favouring the hypothesis that age affects female rejection behaviour. These results have to be interpreted carefully since the age range used here is narrow considering the fact that triatomines could live under laboratory conditions up to one year.

We speculate that rejection behaviour may have as well the function of helping females to choose the appropriate moment to copulate. This hypothesis is plausible if female fitness varies according to at least one internal female factor, such as the ovulatory cycle. Since the ovulatory cycle begins after feeding (Davey, 2007) we compared ex post females which differed in the number of days in which they were starved and were randomly assigned to the treatments. We could not find, however, a relationship between feeding regime and female rejection.

We analysed the relationship between female phenotypic traits (such as thorax length and body weight) and their rejection behaviour. Strikingly, we found that heavier females are significantly less likely to reject males. Interestingly, heavier females in our study were neither better fed nor the largest in terms of physical size. Do heavier females carry more eggs? Are these females at higher risk of ovipositing unfertilized eggs? Whatever the answers, we speculate that mate rejection by females may be related to their ovulatory cycle.

In a recent study, Westerman et al. (2014) examined the effect of a sexual competitor on male–female interactions in the butterfly *Bicyclus anynana* by comparing the behaviour of male–female pairs with that of triads containing either an extra male or an extra female. Strikingly, they found that in the presence of additional individuals mating pairs copulated less than when the couple was isolated, regardless of the direction of sex-ratio skew. Although in our experiment the presence of additional individuals increases female rejection behaviour, both studies suggest that mating behaviour is influenced by the social context, regardless of its sex ratio.

The present work provides empirical evidence showing that an ecological factor such as the availability of potential mates and sexual competitors can affect female selectivity. This result contributes to the idea that female choice is not fixed. Instead, females may adjust their choosiness level according to ecological circumstances.

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