



Original Article

Mobility and mating frequency in the scramble competition polygyny of a chrysomelid beetle

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Received 31 January 2014; revised 1 October 2014; accepted 11 October 2014; Advance Access publication 18 November 2014.

In scramble competition polygyny, male and female mobility may be under strong selection as a result of fitness effects of searching for reproductive resources such as mates, oviposition sites, or resources for egg production. We analyzed the relationship between mating frequency, mobility, and body size in males and females of the chrysomelid beetle *Leptinotarsa undecimlineata*. We obtained a detailed data set of movement and mating frequency of an entire population (1037 adults) over a full reproductive season using individual tagging and direct behavioral observations. Unlike previous studies, we found a negative relationship between mobility and mating success for both sexes. Size was positively correlated to mating frequency in females, but negatively in males. High male mobility may be the result, and not a cause, of low mating success in scramble mating polygynies where rejected or displaced males switch plants more often searching for mating opportunities. More mobile females may be looking for competition-free oviposition substrate and thus experiencing fewer sexual encounters.

Key words: body size, *Leptinotarsa undecimlineata*, mating success, mobility, sexual selection.

INTRODUCTION

Sexual selection is a complex process in which behavior has a prominent role, but the great majority of traits studied as potential targets of sexual selection have been morphological (Kingsolver et al. 2001). For instance, although both body size and mobility are shown to affect mating frequency (Biedermann 2002; Cordero Rivera et al. 2002), much attention has been focused on size (Blanckenhorn 2000), whereas studies relating movement with fitness measures are not nearly as common (Nathan et al. 2008, but see Lane et al. 2010; Moya-Laraño 2010; Glaudas and Rodríguez-Robles 2011; Marmet et al. 2012). Mobility in particular is expected to be an important sexual behavioral trait as it can be correlated with mate encounter rate or mate searching efficiency (Thornhill and Alcock 1983; Schwagmeyer 1988; Shine et al. 2005a; Spritzer et al. 2005a 2005b). This is especially true in scramble competition polygynies (SCPs, Alcock 1980; Dickinson 1992; Nahrung and Allen 2004; Spritzer et al. 2005a 2005b; Barry et al. 2011; Glaudas and Rodríguez-Robles 2011).

What we currently know as SCP was originally defined as explosive breeding assemblages in amphibians and birds (Emlen and Oring 1977; Wells 1977), but the term and definition later suggested by Thornhill and Alcock (1983) for insect mating systems focusing on mate searching was quickly adopted for other animal groups (e.g., Schwagmeyer 1988). Borrowing the concept from Nicholson's (1954) influential concept of "contest" versus "scramble" modes of competition, Thornhill and Alcock (1983) defined SCPs as "nonaggressive searching [...] in which there is an abundance of mates during a limited period or widely dispersed females that cannot be easily monopolized." Even though SCP is likely to be the most common mating system among animals (Barry et al. 2011) and especially among arthropods (Thornhill and Alcock 1983; Dickinson 1992 1995), it is probably one of the least studied (Rank et al. 2006; Barry et al. 2011).

Although it makes sense to consider size within the context of contest competition, which usually co-occur with scramble competition (Parker 2000), the encounter rate should also be important, and this may be influenced by movement rate. Likewise, the role of body size in contests in the context of SCPs may also be relevant but is rarely considered (see Table 1 for exceptions). Therefore, analyses that simultaneously consider size and movement rate

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Table 1
Relationships previously found in SCPs between mobility, size, and mating frequency in males and females

	Mobility	Size	Mating frequency
Mobility	Females	+: No study found –: Moya-Laraño et al. 2007b; Corcobado et al. 2010 0: Biedermann 2002; Kelly et al. 2008	+: No study found –: No study found 0: Nahrung and Allen 2004; Kelly et al. 2008; Glaudas and Rodríguez-Robles 2011
	Males		Females +: Rank et al. 2006 –: No study found 0: Dickinson 1992; Biedermann 2002.
Size	+	+: Hanks et al. 1996; Hegde and Krishna 1997; Foellmer and Fairbairn 2005; Brandt and Andrade 2007; Glaudas and Rodríguez-Robles 2011; Polidori et al. 2013 –: Moya-Laraño et al. 2002, 2007a; Ramos et al. 2004; Kelly et al. 2008; Sztatecsny et al. 2012 0: Goldsmith et al. 1996; Rank et al. 2006; Moya-Laraño et al. 2007a	
	–	+: Hanks et al. 1996; Hegde and Krishna 1997; Biedermann 2002; Cordero Rivera et al. 2002; Bertin and Cezilly 2003; Shine et al. 2005b –: Ghiselin 1974; Andersson 1994; Blanckenhorn et al. 1995, Blanckenhorn 2000; Crompton et al. 2003; Venc 2004; Moya-Laraño et al. 2007b; Kelly et al. 2008 Kasumovic and Andrade 2009; Moya-Laraño et al. 2009; Mendoza-Cuenca and Macías-Ordóñez 2010 0: Dickinson 1992; Nahrung and Allen 2004; Kasumovic et al. 2007; Salavert et al. 2011; Baena and Macías-Ordóñez 2012	Females
Mating frequency	+	+: Alcock 1980; Schwagmeyer 1988; Dickinson 1992; Cordero Rivera et al. 2002; Nahrung and Allen 2004; Spritzer et al. 2005a; Lane 2009 2010; Barry et al. 2011; Glaudas and Rodríguez-Robles 2011; Marmet et al. 2012 –: Baena and Macías-Ordóñez 2012 0: Biedermann 2002; Shine et al. 2005b	Males

“+” and “–” signs group studies depending on the direction of the relationship found; “0” indicates that the authors looked for the relationship but the result was not significant.

can provide valuable insights into the potential trade-offs among behaviors related to success at scramble versus contest competition for mates.

A review of recent literature shows that all potential relationships between male size, mobility, and mating frequency are rarely explored in any given study (see Table 1). Furthermore, among those that have explored these relationships, contrasting results have often been found. Male body size, for instance, has been found to relate positively with mating success in some species but negatively in others (Table 1), probably reflecting the relative importance of contest versus scramble competition in each case. Both positive and negative relationships have also been found between male body size and mobility (Table 1), probably reflecting the relative importance of agility versus endurance. In the case of male mobility and mating success, we could only find reports of positive relationships between these variables (Table 1; but see an exception in Baena and Macías-Ordóñez 2012).

In the case of females, mating frequency is rarely approached in the context of SCPs or any other mating system defined under the male's mechanism of mate acquisition (sensu Emlen and Oring 1977). The term “mating frequency” and not “mating success” is preferentially used in females because a direct relationship with reproductive success, as expected for males, is not to be expected a priori (see Arnqvist and Nilsson 2000). Furthermore, the focus is usually on the relationship between mating frequency, female choice, and reproductive success (fecundity, fertility, and longevity), often measuring tendency to re-mate (under laboratory conditions) more than the natural variation in female mating frequency (Hegde and Krishna 1997; Schäfer and Uhl 2005). Thus, there is

little if any theoretical background and scarce empirical studies relating female body size, mobility, and mating frequency in SCPs. The actual fitness benefit of a given mating frequency for females will depend on the optimum frequency for females of that species or population, which in general has been found to be more than 1 mating event (Arnqvist and Nilsson 2000). Female mating frequency has been found to be positively related to female size, probably as a result of male choice for larger (more fecund) females (Honek 1993; Blackmore and Lord 2000; Bandilla et al. 2008). In SCPs, we could not find a single report of negative relationships between female body size and mating frequency, nor of any significant relationship between mobility and mating frequency (Table 1). Mobility and size, however, have been found to be negatively related (Table 1), likely as a result of more agility of smaller individuals. Even though individuals may differ in their tendency to move (Picman 1981; Switzer 1997), and mobility may be related to mate encounters and thus fertilization rate (Parker 1978; Thornhill and Alcock 1983; Lane et al. 2009 2010; Mori and Evenden 2012), few studies make or test predictions of individual mobility patterns (Saastamoinen 2007; Polidori et al. 2013), especially including females.

Recently, we defined the mating system of a population of the chrysomelid beetle *Leptinotarsa undecimlineata* (Coleoptera) as a SCP, and estimated different proxies of the strength and opportunity for sexual selection throughout the reproductive season (Baena and Macías-Ordóñez 2012). We found fluctuations in the distribution of males and female receptivity, relative abundance, and mobility of males throughout different stages of the reproductive season (for more details, see Study system). In the present study, we aimed to understand the inter-relationship between mobility, body size, and

mating frequency in both sexes. Specifically, we predicted that individuals of either sex that moved more among host plants would also have higher mating frequency as that would increase their encounter rate with potential mates. This may be obvious in the case of males, especially because they do not seem to offer costly ejaculates. In the case of females, however, a positive relationship between these variables would suggest they are following a threshold-dependent mate choice strategy (Beckers and Wagner 2011), in which case those females that move more will find more males above such threshold. Furthermore, we predicted that the relationship between male size and mating frequency would depend on the relationship between size and mobility. Therefore, there would be a small size mating advantage only if smaller individuals were in fact more mobile and male–male contests were relatively less important in female acquisition, as typically suggested for SCPs (Rank et al. 2006). In the case of females, we would expect larger females to mate more frequently as a result of male preference for larger (more fecund) females (Honek 1993; Blackmore and Lord 2000; Bandilla et al. 2008).

METHODS

Study system

After spending the period between reproductive seasons underground, adults of *L. undecimlineata* emerge in the summer. Individuals are mostly active during daylight hours, when all reproductive activities take place (Baena ML, Macías-Ordóñez R, personal observation). They exclusively use *Solanum lanceolatum* Cav. and *S. chrysostrichum* Schltdl. as larval and adult feeding resource, as oviposition resource for females, and as mating site. In fact, individuals (both adults and larvae) spend the entire reproductive season on these 2 host plants and are commonly not found on the ground or any other substrate. Both males and females mate with different mates, and may mate repeatedly with the same mate. Females frequently oviposit after mating and males usually stay on or near the female, seemingly guarding and/or courting her, and then copulate again. This copulation-oviposition sequence with the same male may be repeated up to 13 times during up to 4 h. Males seem to court females before and after copulation, and we did not observe any male–female interaction that suggested forced copulation. Although females are clearly larger than males, no other secondary sexual character is evident in either sex. The new cohort of adults may mate during the season they hatched and then bury themselves until the following season. Many individuals are present for only some fraction of the reproductive season, either because they last to molt to adult, die, bury, or leave the sampling area, either permanently or temporarily (Baena ML, Macías-Ordóñez R, personal observation).

Study site and data collection

The study was carried out between 21 July and 7 November 2004 in a secondary forest replacing a pasture grassland abandoned for 7 years at the time of observations. The site is close to a fragment of cloud forest at a location known as El Riscal, in Central Veracruz, Mexico (19°28'56"N, 96°59'48"W, 1595 m asl). The mean annual temperature is 20 °C (min = 12 °C, max = 34 °C) and annual precipitation more than 3000 mm (Soto and Gómez 1990; Holwerda et al. 2010). The studied population was found on a patch of 75 adult plants and 278 nonsexual juvenile plants of *S. lanceolatum* and 8 plants of *S. chrysostrichum* in an area of about 400 m². Host plants were individually marked with aluminum tags. Beetles were individually marked using numbered and color-coded

queen honey bee tags (2 mm in diameter). The right or left elytron, depending on sex, was lightly scratched with sand paper and then the tag was glued with Instant Crazy Glue®. A total of 660 males and 377 females were tagged. Each individual was measured using a calliper (\pm 0.1 mm). Body size was defined as thorax width for both sexes as an estimate of structural body size, that is, a measure that does not depend on nutritional condition or reproductive state (Green 2001; Barry et al. 2011).

All individuals present on all plants were recorded daily over the whole reproductive season (95 days). For analytical purposes (see below), the reproductive season was divided in 5 periods (1: days 6–25; 2: 26–45; 3: 46–65; 4: 66–85; 5:86:95) based on clear changes in the reproductive dynamics along the reproductive season (Baena and Macías-Ordóñez 2012). Censuses were carried out by visual inspection of each plant along the same route, but alternating the starting and ending point every day to avoid any bias due to the effect of time of day. All behavioral records were carried out in observations of 30 min per plant, on all plants hosting at least 1 adult individual of each sex, between 8:00 and 18:00 Central Standard Time (GMT-6). A mating event was recorded if a mount was observed and aedeagus intromission was recorded to last at least 5 min (preliminary observations revealed frequent intromissions of very short duration, frequently among males, that we assumed as failed attempts; such time criterion seemed to eliminate most of them). Repeated copulations with the same mate between oviposition events recorded during each 30-min observation period were not recorded as additional mating events.

We defined mobility as “plant switch rate,” that is, the number of plants each individual occupied in any given period divided by the number of days the individual was observed in such period. We opted for not using distance-based speed estimations due to their high dependence on number of recaptures and questionable biological meaning (Samietz and Berger 1997). It is important to point out that individuals that were not present during a given period, did not result in records during such periods. However, the number of days each individual was present in a given period was variable and could be expected to relate positively with mating frequency, therefore, it was included as a covariable in all analyses as “presence.”

Statistical analyses

Generalized linear mixed-effects models (GLMMs) implemented in the *lme4* library version 1.1–6 (Bates et al. 2011) of the R statistical software version 3.1.0 were used for all analyses (R Development Core Team 2008). In order to assess mobility as predictor of mating frequency (number of mating events per individual per period), we performed a GLMM on male and female mating frequency, using plant switch rate as explanatory variable. Presence and thorax width were also included as covariables (fixed factors) in the analyses, whereas period (as repeated measure) was defined as random factor. A Poisson error distribution and logarithmic transformation as link function were declared in both statistical models of mating frequency. Only second-order statistical interactions were included (as fixed factors).

Similarly, in order to assess the relationship between sex, size, and mobility, we performed a GLMM on plant switch rate. Sex (factor with 2 levels, male/female), presence and thorax width (covariables), and second-order interactions were set as fixed factors, whereas the random component of the model was also defined as explained previously. We defined a Gaussian error distribution and link function identity.

Finally, in order to further explore the result obtained between male size and mating frequency (see below), we assessed the relationships between male size and presence, and between male size and mating rate (mating frequency/presence). In both analyses, the only independent variable was male thorax width, and the structure of the random component was similar to previous analyses. A Poisson error distribution was used for the analysis on presence, and a binomial error distribution for the analysis on male mating rate.

As analysis of variance (Anova) tables are not yet implemented for GLMMs under Poisson error distribution, significance of main factors and interactions for all tests were obtained via model simplification and Anova tests between models based on the chi-square distribution of the deviance. Using the same procedure, we tested the significance of the interaction between sex and the independent variables in the analyses on mating frequency in order to compare the slope of the models of each variable between sexes. To minimize interference of nonsignificant factors, standard errors were calculated from simple models including only 1 significant factor or covariable (Crawley 2002).

No ethics approval was required as no animals were sacrificed or collected.

RESULTS

Out of 660 males and 377 females recorded, 635 (96.2%) males and 343 (91%) females were recaptured at least once, and 404 (63.6%) males and 262 (76.4%) females copulated at least once in the reproductive season. Over one-third of the males (231 out of 635), did not mate at all; 178 (28%) mated once, whereas 226 (35.6%) copulated twice or more.

Mating frequency per period

Contrary to our predictions, plant switch rate was negatively correlated to male and female mating frequency (Figure 1), and its statistical interaction with sex was also significant (Table 2), suggesting a stronger relationship for females. The models predicted nearly 0 mating events per period for the individuals that moved at a higher rate (0.076 for males and 0.032 for females), more than 1 (1.203) mating event per period for the males that moved less, and more than 2 (2.349) mating events per period for the females that moved less.

Thorax width, however, showed a positive relationship with female mating frequency per period, but a negative one (although almost flat) with male mating frequency per period (Figure 2). The predicted difference in mating frequency per period between the smallest (0.713 mating events per period) and the largest females (1.502 mating events per period) was about 2-fold, whereas the predicted difference between the smallest (0.631 mating events per period) and the largest males (0.593 mating events per period) was only about 6%. As could be expected from this, the statistical interaction between thorax width and sex was significant (Table 2).

Not surprisingly, male and female presence was positively associated with mating frequency (supplementary figure S1). The models predicted nearly 0 mating events per period for the individuals that were present just 1 day during the period (0.189 for males and 0.235 for females), less than 2 (1.785) mating event per period for the males that were present the whole period, and more than 2 (2.348) mating events per period for the corresponding females. However, the lack of significance of the statistical interaction with sex (Table 2) suggests that the effect of the number of days present in a given period on the number of mating events in that period does not differ between males and females.

None of the second-order interactions between plant switch rate, thorax width, and presence as factors of mating frequency per period were significant for either sex (Table 2).

Mobility

Sex, size, and presence were all significant predictors of plant switch rate, but none of their statistical interactions were significant (Table 3). Model's predictions suggest that females switched plants at a very slightly lower rate (0.592 plants per day) than males did (0.593 plants per day). The model also predicted that the smallest individuals moved somewhat faster (0.650 plants per day) than the largest ones (0.488 plants per day; Figure 3a), and that individuals that were present for just 1 day during the period switched plants more than 3 times faster (0.815 plants/d) than those present for the whole period (0.234 plants/d) (Figure 3b).

Male size versus presence and mating rate

Size was a significant predictor of both presence ($\chi^2 = 138.44$, g. l. = 1, $P < 0.001$) and male mating rate ($\chi^2 = 23.767$, g. l. = 1, $P < 0.001$). The models suggest a 2-day difference in number of days present in each period between the smallest (9.57 day) and the largest males (7.77 day; Figure 4a), but a clearly opposite trend in the mating rate as the smallest males mated at a much lower rate (0.016 copulas per day) than the largest males (0.267 copulas per day; Figure 4b). It is worth noticing 2 outliers on the right side of

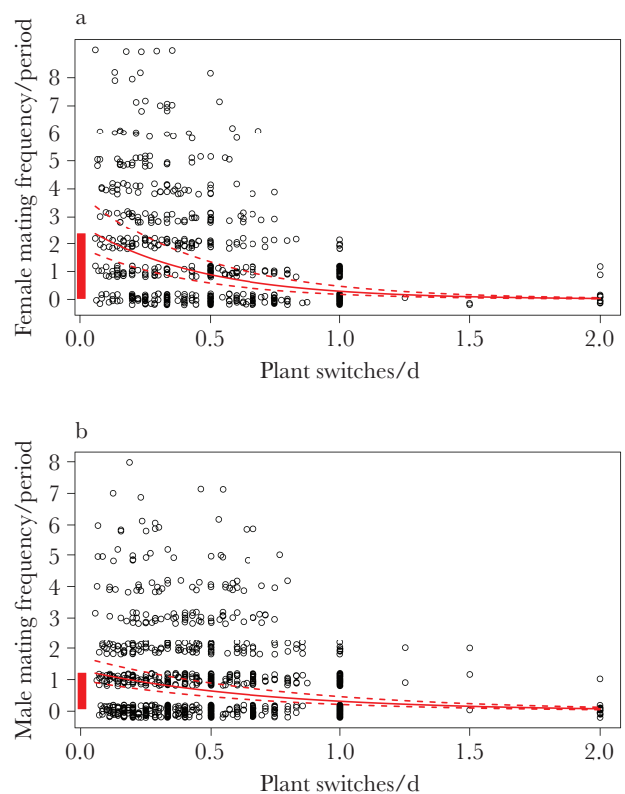


Figure 1 Plant switch rate versus female (a) and male (b) mating frequency per period. Observed values (circles) have been jittered to avoid overplotting. The relationships predicted by the GLMMs (solid lines) and their standard errors (broken lines) show that plant switch rate is negatively related to mating frequency in both sexes. Solid bars next to the y axis show the range of y values predicted by the models along the observed ranges of x values.

Table 2
Predictors (fixed effects) of mating frequency in males and females of *Leptinotarsa undecimlineata*

Analysis	Fixed factor	χ^2	df	<i>P</i>
Male mating success	Plant switch rate	9.388	1	0.002
	Size	48.774	1	<0.001
	Presence	363.380	1	<0.001
	Plant switch rate \times Size	0.176	1	0.675
	Plant switch rate \times Presence	0.426	1	0.514
	Size \times Presence	0.000	1	1.000
	Female mating success	Plant switch rate	94.373	1
Female mating success	Size	60.245	1	<0.001
	Presence	223.750	1	<0.001
	Plant switch rate \times Size	0.163	1	0.686
	Plant switch rate \times Presence	2.081	1	0.149
	Size \times Presence	0.000	1	1.000
Interactions sex vs.	Plant switch rate	23.046	1	<0.001
	Size	4.789	1	0.029
	Presence	0.092	1	0.762

Significant *P* values are highlighted in bold.

Table 3
Predictors (fixed effects) of individual mobility in *Leptinotarsa undecimlineata*

Analysis	Fixed factor	χ^2	df	<i>P</i>
Plant switch rate	Sex	10.021	1	0.002
	Size	11.659	1	<0.001
	Presence	739.920	1	<0.001
	Sex \times Size	1.813	1	0.178
	Sex \times Presence	1.628	1	0.202
	Size \times Presence	2.964	1	0.085

Significant *P* values are highlighted in bold.

(i.e., all variables and interactions were either significant or nonsignificant with or without inclusion of the 2 outliers).

DISCUSSION

Our aim to explore the relationship between mobility, size, and mating frequency for both males and females throughout a full reproductive season resulted in some unexpected and puzzling patterns. Plant switch rate was negatively associated with male and female mating frequency (Figure 1), which could be revealing different aspects of mate searching, a topic frequently ignored (reviewed in Ceballos Meraz et al. 2011). Among males, a negative relationship is not consistent with previous findings in other species, which suggest that male mobility in SCPs should be positively correlated with mating success (see Table 1). One interpretation of the inverse relationship between male mating frequency and plant switch rate may be that smaller (low-quality) males switch plants more often (Figure 3a) searching for mating opportunities, either because they are rejected by females or excluded by larger males. On the other hand, larger (high-quality) males would not need to switch plants as much and may even monopolize them to some degree (Baena and Macías-Ordóñez 2012). Therefore, high mobility would be a result of low mating success, which is consistent with our finding that large males and males that were present for more days in a given period, and thus had higher mating frequency (supplementary figure S1), were also moving at a lower rate (Figure 3). However, we found that small and more mobile males (Figure 3a) were slightly more successful in acquiring mates than large males (Figure 2b).

In SCPs, selection for high mobility of small males occurs when females are scarce, disperse, or unpredictable (Thornhill and Alcock 1983). This theoretical prediction has some empirical support for spiders (Baruffaldi and Costa 2010), mantids (Barry et al. 2011), and snakes (Glaudas and Rodríguez-Robles 2011). In our study system, however, females seem to be abundant and their occurrence is highly predictable because they are found exclusively on 2 conspicuous and spatially aggregated species of host plants. In some systems, small males have been shown to have a mating advantage due to higher mobility (Blanckenhorn 2000; Crompton et al. 2003; Moya-Laraño et al. 2007b; Mendoza-Cuenca and Macías-Ordóñez 2010; Salavert et al. 2011). In *L. undecimlineata*, however, males do not race but occasionally fight each other over copulating or ovipositing females (Baena and Macías-Ordóñez 2012). This inconsistency may be explained by the fact that large males do mate at a higher rate than small males (Figure 4b), but this advantage is not enough to counterbalance the longer presence of small males (Figure 4a), that is, more time to obtain mates albeit at a lower rate, thus resulting in a still negative although nearly flat relationship

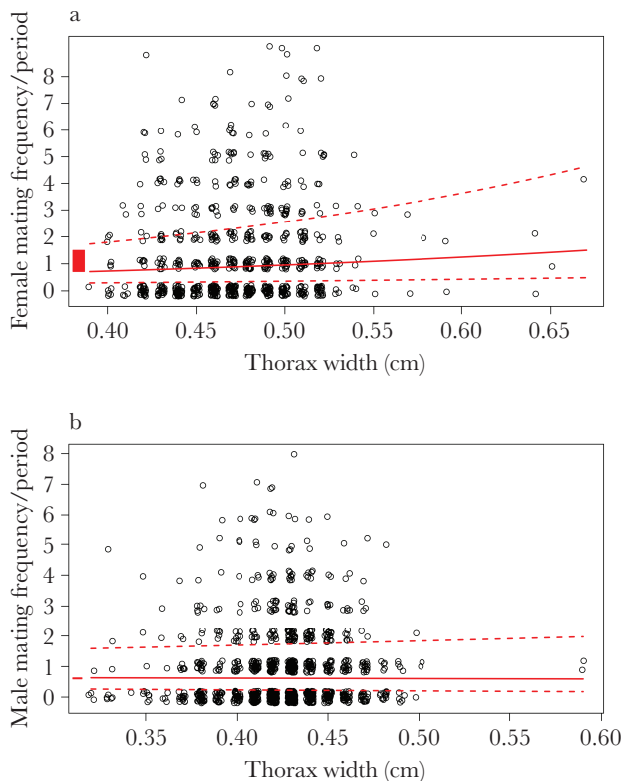


Figure 2
Thorax width versus female (a) and male (b) mating frequency per period. Observed values (circles) have been jittered to avoid overplotting. The relationships predicted by the GLMMs (solid lines) and their standard errors (broken lines) show that thorax width is positively related to female mating frequency and negatively to male mating frequency. Solid bars next to the *y* axis show the range of *y* values predicted by the models along the observed ranges of *x* values.

Figure 4a,b, which could seem to be determinant in the tendency of the analysis of the whole data set. In order to eliminate this possibility, all analyses were repeated excluding those data points, and although there were slight differences in the statistical values, to be expected, there were no changes in any of the conclusions derived

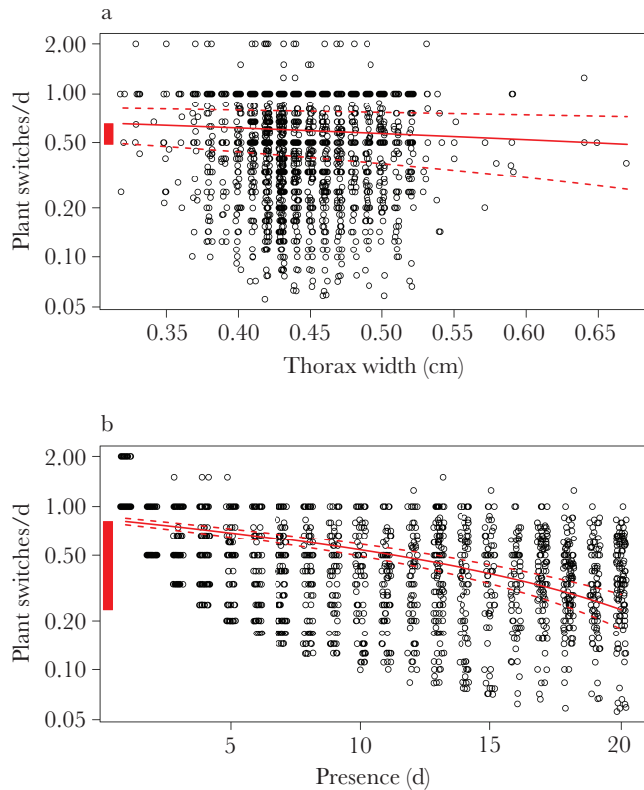


Figure 3 Thorax width (a) and presence (b) versus plant switch rate. Observed values (circles) have been jittered to avoid overplotting. The relationships predicted by the GLMMs (solid lines) and their standard errors (broken lines) show that plant switch rate is negatively related to thorax width and presence. Solid bars next to the y axis show the range of y values predicted by the models along the observed ranges of x values.

between size and mating success. Small males may have longer presence for different reasons including faster development, lower nutritional requirements and lower mortality (reviewed in Blanckenhorn 2000), or delayed overwintering onset due to higher risk of mortality of small individuals during such period, as found in other coleopterans (Osawa 2002; Smith 2002).

It is noteworthy that a previous study (Baena and Macías-Ordóñez 2012) did not find a size-related male mating advantage when analyzing the same data set using mating differentials (Jones 2009). This suggests that standard methods that assess the strength of sexual selection may lack the sensitivity to detect such small effects as those found in this study (around a 6% difference between the largest and the smallest males). The fact that mixed-effects models may be more sensitive than selection differentials is intriguing, especially due to the fact that the former are actually conservative when controlling for nonindependent data points, thus avoiding pseudoreplication.

Results for females are also somewhat puzzling. Unlike males, females do not fight and they are not expected to be sperm limited as males often copulate repeatedly with an ovipositing female. Basic sexual selection theory suggests that, unlike males, low mating frequency usually does not translate into a reproductive cost for females (Arnqvist and Nilsson 2000). Larger and less mobile females (Figure 3a) seem to be present for longer intervals (Figure 3b) and be sought by (and accept) more males (Figures 1a and 2a), which also would promote multiple paternity and sperm

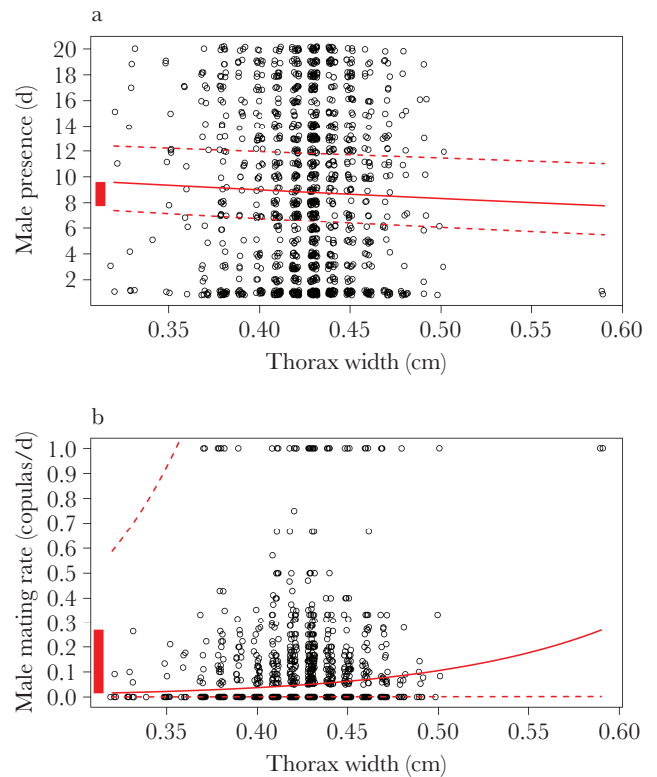


Figure 4 Male size versus male presence (a) and mating rate (b) per period. Observed values (circles) have been jittered to avoid overplotting. The relationships predicted by the GLMMs (solid lines) and their standard errors (broken lines) show that male size is negatively related to presence, but positively related to mating rate. Solid bars next to the y axis show the range of y values predicted by the models along the observed ranges of x values.

competition. Smaller females may move more looking for plants with fewer females and thus less potential competition for their smaller clutches. In such case, lower mating success of smaller female may also be due to lower male density in plants with fewer females, and/or male preference for larger females. All this would suggest that, at least in *L. undecimlineata* and similar populations of high-density phytophagous insects with SCP, movement may have little to do with mate searching. In another phytophagous insect with SCP, the homopteran *Cercopis sanguinolenta* (Biedermann 2002), mating frequency was found to be associated with body size but not mobility. As we suggested here for *L. undecimlineata*, adult movements in this homopteran seem to be unrelated to mate searching, but may have a role in finding food (Biedermann 2002).

We found such a small difference between sexes in mobility (0.001 plants per day) that this may be a by-product of an unusually large sample size. We suggest that no major sexual difference in mobility has to be expected in polygynous mating systems if both sexes can predict the location of potential mates and reproductive resources, unless resource monopolization by 1 sex results in higher or lower mobility of the other. Such is the case of the harem-defending tree weta *Hemideima crassidens* (Kelly 2006) in which females avoid male-occupied resources. However, as far as we know, a lack of sex differences has only been described during the nonreproductive season in SCP mating systems (e.g., *Crotalus mitchellii*; Glaudas and Rodríguez-Robles 2011). Our results suggest that a sex-biased investment in mate searching may not be the rule.

Moreover, assuming that male movement during the reproductive season is mostly due to mate searching in SCPs may be misleading. In fact, unlike predictions for many SCP mating systems (Trivers 1972; Thornhill and Alcock 1983; Brown and Weatherhead 1999), *L. undecimlineata* females do not move at a biologically meaningful lower rate than males, probably due to the need of resources to meet the energetic cost of egg maturation (Saastamoinen 2007). Both adults and larvae can quickly strip even a large plant of edible tissue, and the reproductive costs for females of insufficient foraging may be higher than for males. As suggested previously, females may therefore move more while searching for food resources for themselves to produce eggs, and/or suitable oviposition sites with enough food for the larvae. In contrast, males of the congeneric species *L. lacerata* do spend more time “searching for mates” than females (Osorio-Beristain et al. 2004). Although the function of the described movement was not assessed in such study, if males in fact search for females they may be responding to either low female density or low female aggregation.

Among the few attempts to assess the relationship between mating frequency and mobility, results are inconsistent (Table 1). As reviewed by Parker (2000), there may not be pure contest or scramble competition, but always a mix of both in different proportions. We suggest that the same holds true when these concepts are applied to modes of competition over reproductive resources such as mates (i.e., mating systems). In scramble-like mating systems such as SCPs, contests with absolute winners and losers may play a more or less important role in the final distribution of resources (mates). Scramble level is predicted to increase when resources increase with the number of competitors, that is, the amount of resources per capita is held constant (Parker 2000). It means that under relatively constant sex ratios, as occur in *L. undecimlineata* (Baena and Macías-Ordóñez 2012), scramble competition among males should covary with male density throughout the reproductive season (see Kokko and Rankin 2006). In other SCPs, scramble competition among males (“scramble level” sensu Parker 2000) may be more significant than any direct male–male interaction and thus a small male mating advantage due to higher mobility of smaller males may be expected.

“Scramble competition polygyny” is a term broadly applied to different types of superficially SCP-looking mating systems. Even though some females may mate as often or more than any male (most of which could even be monogynous), males may also be defending mate or resources at some point, and alternative reproductive tactics may be involved. Furthermore, it may be very hard to find a pure SCP, that is, nonpolygynandrous (monandrous females usually elicit some form of female and/or site defense, which is not scramble-like by definition), and with no contest competition for mates involved at all.

Unlike males of previously studied SCPs, males of *L. undecimlineata* are not clearly more mobile than females. Different grades of scramble competition should be considered depending on the relative importance of “scramble” versus “contest” inter- and intra-sexual interactions. We suggest that future studies of SCP should not assume that movement rate is related only (or primarily) to mate searching effort, at least in populations in which females are not dispersed. In these systems, aggregation of female receptivity may be hard to monopolize, but may still elicit male–male competition similar to that found in resource-based mating systems. In SCP with moderate to high aggregation of female receptivity or density, movement rates may be a by-product of intra-sexual biases in mating frequency.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

FUNDING

This study was partially supported by Consejo Nacional de Ciencia y Tecnología (No. 204950).

This study was part of the doctoral dissertation of M. L. Baena at the Doctorado en Ecología y Manejo de Recursos Naturales, Instituto de Ecología, A. C. The manuscript benefited from comments by J. Rull, D. Pérez, C. Cordero, K. Collie, L. Sirot, R. Guevara (who also gave us generous and extensive statistical advice), 2 anonymous reviewers, and our Handling Editor. We also thank F. Escobar, S. Falqueto, E. Matla, and P. Dámanos for logistical support.

Handling editor: Glauco Machado

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