Apidologie (2022) 53:9
© The Author(s), 2022
https://doi.org/10.1007/s13592-022-00916-7

Original article

Mating behaviour of the large-head resin bee *Heriades truncorum* (Megachilidae: Osminii) suggests female plastic strategy in selection of a mating partner and male quality assessment

Samuel Boff[1,2]

[1] Animal Ecology and Tropical Ecology, University of Würzburg, Am Hubland, 79074 Wurzburg, Germany
[2] Evolutionary Ecology and Conservation Genomics, Ulm University, Albert-Einstein-Allee 11, 89081 Ulm, Germany

Received 9 August 2021 – Revised 30 November 2021 – Accepted 16 January 2022

Abstract – Behavioural courtship display and size of males are two attributes often used by females to select a mating partner. According to sexual selection, such traits are of importance, because a bigger size male or males displaying a better courtship could enhance the possibility of females to transmit her genes to the following generations via her offspring. In Hymenoptera such as in solitary bees, it is known that females can assess male quality and add this information in the process of mating choice. In the current study, I describe aspects of pre-copulatory mating behaviour of males, male quality assessment and female choice in the large-headed resin bee *Heriades truncorum* (Hymenoptera: Megachilidae: Osminii). Males of *Heriades truncorum* perform thoracic vibration, fan their wings and lift upwards female's abdomen to copulate. Couples engage in sideways rocking motion movement like a dance. Female selection of a partner was also found to be density dependent. In a pair situation (one female for one male), female copulate equally with males of all sizes and male mating effort enhanced the chance of successful copulation. In an environment with mating choices (one female for two males of different sizes), successful copulation was significantly more frequent for bigger size males. Female response to male mounting took place independently of the number of mating partners in the arena and did not impair mating. Additionally, size had no effect on male-male competition. Both results suggest mating success in *Heriades truncorum* rely on a female choice mechanism.

Copulation / Courtship / Female choice / Mating attempts / Body size / Male density

1. INTRODUCTION

Mating behaviour strategy including male courtship display, as well as the interference of body size in mating, are primary goals to understand evolutionary aspects of mating success and female choice (Alcock 2013). In several animal species, mating behaviour includes a selective initial phase when males display a pre-copulatory behaviour. This initial mating phase can include movement of body parts, followed by ritualized performances (Alcock 2009). Successful copulation can be widely attributed on the quality of its performance through female choice (Von Schantz et al. 1989; Ayasse et al. 2001; Takeshita and Murai 2016) and density of potential partners (Kokko and Rankin 2006; Lehmann 2007; Atwell and Wagner 2014).

In insects, pre-copulatory behaviour is often used by males to attract mating partners. In this selective

---

Corresponding author: S. Boff,
samuel.boff@uni-ulm.de
Manuscript editor: Peter Rosenkranz

scenarios' chosen males may overcome the mating behavioural display from those displayed by less successful competitors. For example, male crickets (Grylloidea) produce sound to attract females by rubbing their wings together, and success may depend on the ability of males to sonicate it according to female request (Mhatre et al. 2012). Similarly, male fruit flies (Drosophilidae) vibrate the wings in pre-copulatory behaviour producing a song that is used by the female to assess male quality (Hoikkala et al. 1999). In Hymenoptera, such as solitary bees, males are also known to display sexual signals used by female to assess male quality. For instance, females of *Osmia bicornis* (Osminii) are known to use the male's thoracic vibrations to assess male quality during courtship (Conrad et al. 2010). Male body size has also been found to be correlated with male success in solitary bee species performing scramble competition (Ayasse et al. 2001; Russell et al. 2018) which predicts that a finite resource (e.g. females) is similarly accessible to all competitors.

In the sexual selection context, females could preferentially copulate with males possessing behavioural traits that could enhance the possibility of the female to transmit her own genes through sexual reproduction via her offspring to the following generation. Moreover, individuals of bigger size may be favoured either due to relative female choice or to male–male competition (Savalli and Fox 1998; Koffler et al. 2016). Documentation on the aspects of female choice and male pre-copulatory display in solitary bees is limited to a few species (Alcock and Johnson 1990; Paxton 2005). However, it mostly focused on males and their behavioural display and the passive process of female quality evaluation carried on to final decision: acceptance or rejection of a male (Conrad et al. 2010). Therefore, investigation on these parameters especially in rarely studied bee species is an opportunity to understand female bee decision-making (strategies of a mating partner) and therefore deepening our knowledge on aspects of sexual selection for rarely studied wild bee species.

Heriades truncorum (Linnaeus, 1758) is a small (6–8 mm length) solitary bee species belonging to the family Megachilidae (Osminii). This species is a cavity nesting bee with brood cells arranged in linear series with number of brood cells ranging from 2 to 16 (Maciel de Almeida Correa 1981). Females make a space between the last brood cell and nest entrance and enclose it with resin (Rozen and Praz 2016). The species is widespread across Central Europe with its natural distribution extended to arid zones of Northern Africa and Western Asia (Michez et al. 2019). The bees are univoltine, active mostly from June to August. They are oligolectic, and females are mostly associated with Asteraceae flowering from where they collect pollen by tapping its abdomen on pollen-presenting florets (Konzmann et al. 2020), while active during European summer (Praz et al. 2008). Recently, it was shown that individuals of *H. truncorum* are mostly restricted to its local environment due to its short flight distance (Hofmann et al. 2020).

In the current study, I describe to *Heriades truncorum* aspects of male pre-copulatory behaviour, which includes thoracic vibration, wing fanning, sideways rocking motion and lift upwards female's abdomen to copulate. Wing fanning, a pre-copulatory behaviour displayed before mating, was investigated across individuals of different localities to test for fixed action pattern. I hypothesize if wing fanning increases the chance of a given male to succeed in copulation and this behaviour has been selected, the frequency of males displaying wing fanning would be higher than those males not performing wing fanning. Additionally, I tested if mating attempts and individual sizes are predictors of copulation. I hypothesize that increasing the number of mating attempts increases the chance to successfully perform copulation, as shown in other arthropods (Shamble et al. 2009), because persistence (and continuous courtship display) might be an indicator of male quality. Moreover, if size is a trait of relevance and female process phenotypic information, copulation would favour individuals of bigger sizes. I also test whether male size affected the number of attempts that were necessary for copulating to understand the relation between male reproductive effort, their sizes and female choice.

From my preliminary observations in the species mating behaviour, females respond to male mounting either by biting or by using her hind legs towards males. Thus, I tested if the female response to male mounting varies depending on male successful copulation. If female response has a significant negative effect over copulation, this probably could indicate that female response to male mounting works as mating avoidance behaviour. Yet, if this interaction does not completely impair copulation, female response to male mounting is a case of female evaluation of male quality. Since hymenopteran females, including close related species of Osminii, are known to evaluate male quality (Ayasse et al. 2001) and reject males by pushing males off from its back (Conrad and Ayasse 2015), I suspect females of *H. truncorum* to evaluate their mating partners as well. Finally, if male-male competition in *H. truncorum* is dependent on male size (Russell et al. 2018), smaller males would fail to interfere in mating situations with bigger conspecifics.

2. MATERIAL AND METHODS

2.1. Preliminary observation and description of the mating behaviour

Several females and males of *H. truncorum* were placed all together in a flight cage (40 × 40 × 60 cm) in the presence of a flowering plant of an Asteraceae species (*Ajanja pacifica*). Individuals of both sexes were randomly observed, and mating attempts (male seeking a female and performing a fast-grabbing behaviour) and copulations (insertion of male genitalia into female) were observed in the cage. To quantify these behavioural approaches, freshly emerging males and females of *H. truncorum* from phragmites stems (collected from several sampling areas in Bavaria (Figure 1), south of Germany) were placed individually in petri dishes (2.5 cm Ø, 1.5 cm high) and let to feed ad libitum in a feeder with sucrose solution 50% up to 3 days. The intertegular distance of random males ($n = 40$) and females ($n = 41$) was sized with the software Las Ez version 3.4.0 attached to a stereomicroscope (Leica EZ4D). The studies were performed following natural emergence of individual in lab environment (Department of Animal Ecology and Tropical Biology, University of Würzburg) from July to August 2020.

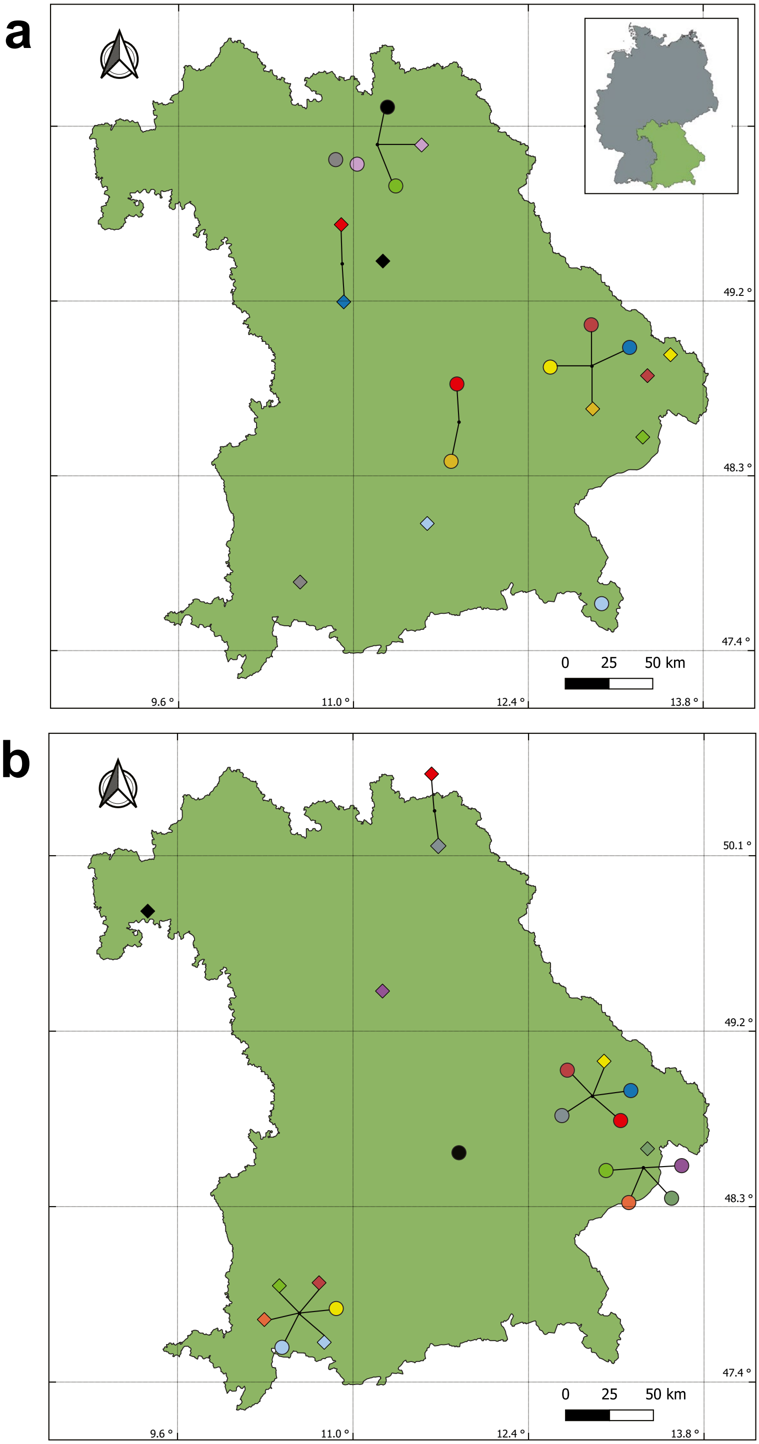
2.2. Assay 1: In pair situation

One male and one female were randomly chosen from different localities (Figure 1a) and were inserted in a petri dish (dimensions: 5.5 Ø, 1.5 cm high). I followed mating activities of 10 pairs for a period of 15 min each (except two videos of 6 min each), totalling 142 min of observations. In this experiment, I quantified the number of mating attempts, the average time males remained mounted over the females and the number of copulations.

2.3. Assay 2—Mating choice experiment

Two males of *H. truncorum* from the same sampling sites were marked with non-toxic colours (edding®) and inserted in a petri dish (5.5 cm Ø and 1.5 cm high) following the insertion of a freshly emerged female from a different sampling locality (Figure 1b). Males of same sampling site were inserted into the arena to minimize female choice based on non-measured traits relative to a specific site (Vereecken et al. 2007). The interactions between a given male and the female were recorded for a period varying between 7 and 11 min. A total of 11 trials with one female and two males ($n♂ = 22$ and $n♀ = 11$) were recorded totalling 51 min of observations. Recording with a camera gave the possibility to observe, in addition of mating attempts, and the number of events a given male displayed wing fanning, copulation events, female response to male mounting (Online Resource, Video 1) and mating interruption by action of the conspecific male.

All females and males used in the mating experiment were sized my measuring their intertegular distance, and this information was used in the models as predictor variables.


a
49.2 °
48.3 °
47.4 °
0 25 50 km
9.6 °
11.0 °
12.4 °
13.8 °
b
50.1 °
49.2 °
48.3 °
47.4 °
0 25 50 km
9.6 °
11.0 °
12.4 °
13.8 °

◂**Figure 1.** Individuals of *Heriades truncorum* were obtained with the aid of trap nests from different areas of Bavaria region, Germany. **a** Assay 1: Mating in a pair situation. Circles correspond to males, and diamonds correspond to the females. Colours indicate the origin of the mating pair. **b** Assay 2: Mating choice experiment. Each circle represents two males used in the same trial; the diamond corresponds to the females. In both figures, colours indicate the origin of a given bee, note that males and females used in each trial were always originally from different sampling site. The origin of the female used in the assay 2 with males represented by blue colour is unknown

2.4. Statistics

The size of females and males was compared with t test.

2.5. Assay 1—Mating in a pair situation

I used generalized liner models (GLMs) to analyse if the number of mating attempts depend on the size of the mating partners with Poisson error distribution. Also, I used a GLM with successful copulation (0 = rejection, 1 = copulation) as response variable and the number of mating attempts and size of males as fixed factor with binomial error structure. Size of the mating partners did not affect copulation; therefore, this variable was excluded for a better fit of the model.

2.6. Assay 2: Mating choice experiment

I tested if the size of the mating partners (female and male) influences mating attempts with a GLM and Poisson error structure. I used a GLM with female response to male mounting (bites), the time a given male remained mounted over the female and male size as fixed factors and binomial error structure to test the effect of these variables in successful copulation (0 = rejection, 1 = copulation). Fixed factors were considered based on lowest value of AIC. I tested if wing fanning is a commonly displayed behaviour by comparing with a binomial test the frequency of males displaying this behaviour across different sites. To explore if the number of mating attempts predicts successful copulations, I built up a dataset by summing up all mating attempts of a given male. I used a GLM with successful copulation as response variable and the total number of mating attempts per male as fixed factor with binomial error structure. To test whether male size (fixed factor) affected the number of attempts that were necessary for copulating (male reproductive success), I used a GLM with male reproductive success as response variable and quasi-Poisson error distribution. Male reproductive success ranged from values between "0" and "1," with higher indicating higher reproductive success. A correlation (Pearson) between mating attempt and female response to male mounting was tested with the aim to acquire information on the magnitude of potential action/reaction measures. Lastly, I test with a GLM if male interference (response variable) over the formed couple led to male partner replacement using the size of male as fixed factor. All statistics were produced with software r (R Core Team 2018).

3. RESULTS

Females of *H. truncorum* were significantly bigger ($N♀ = 40$, mean ± s.d = 1.49 ± 0.1 mm) than males ($N♂ = 39$, mean ± s.d = 1.32 ± 0.11 mm) (t test, $t = 7.02$, df = 76.95, $p < 0.0001$, Online Resource, Figure S1).

3.1. Description of male pre-copulatory behaviour

Individuals of both sexes were actively moving in the petri dish. The females usually explored the petri dishes with their antennal flagella distended. The males explored the arena with the last two segments of their antennal flagella curled and touching the ground while moving. The males were observed displaying a turning movement by changing the direction towards the females, and eventually interacting with them by performing an attempt to mate. The attempt to mate was displayed as a fast movement of grabbing the female followed by mounting over her. The common position is the males hold the females including the use of the second and the third leg pairs to hold the abdomen of the female (from second tergite/sternite (T2/S2) to fourth tergite/sternite (T4/S4) with their second and third pairs of legs). Bigger males were observed holding females on the first tergite segment (T1). The males then fanned their wings intermittently and held the mating partner mostly in an ~ 85° angle in relation to the female body (Online Resource, Figure S2a). The males always held their first pair of legs up without touching the females (Online Resource, Figure S2a, b). Wing fanning was performed regularly, as well as thoracic vibrations.

During male wing fanning, the mating pair did not fly away, rather the male lifted up the female's abdomen (Online Resource, Figure S2b), and together, they displayed an alternated movement leading the couple to perform a movement of sideways rocking motion to the right and left side repeatedly similar to a dance (Figure 2; Online Resource, Video 2). Sideways rocking motion precedes copulation events. After copulation, the male released the female and immediately after retracted its genitalia.

3.2. Assay 1: Mating in pair situation

The number of mating attempts was independent of females and male body sizes (GLM; χ^2♀ $= 0.08$, df $= 1$, $p = 0.76$; χ^2♂ $= 0.62$, df $= 1$, $p = 0.42$). Males spent in average 105 ± 151 s mounted over the female in 13 records. Copulations were recorded to 50% of the mating couples ($n = 5$) and it was dependent on the number of mating attempts (GLM, $\chi 2 = 5.62$, df $= 1$, p $= 0.01$: Figure 3). Successive copulations were recorded only for two couples.

3.3. Assay 2: Mating choice experiment

In the scenario with male options, mating attempt was performed by all males. In average, males performed 2.09 ± 1.1 mating attempts. The number of mating attempts was independent of size of females and males (GLM; χ^2♀ $= 0.224$, df $= 1$, $p = 0.635$, χ^2♂ $= 0.045$, df $= 1$, $p = 0.830$). Wing fanning was performed by males of all localities. The frequency of males performing wing fanning (82%) was significantly higher than of males that did display the behaviour (18%) (binomial test, $p = 0.004$: Online Resource, Figure S3). Sideways rocking motion and lifting female abdomen are followed by pre-copulatory behaviour and were displayed at lower frequency (50 and 32%, respectively), and difference was not significant between individuals displaying or not these behaviours ($p = 1$ and $p = 0.318$, respectively). Copulation was observed in 70% of the mating groups. Female copulation with multiple males was recorded only once. Mating attempts seemed to be less important in an environment with two males since it had no effect in successful copulation (GLM; $\chi^2 = 2.19$, df $= 1$, $p = 0.13$).

Interruption performed by a given male towards a mating pair during pre-copulatory phase (male replacement) occurred in 14 out 43 times that a couple was formed. In 100% of the cases, the interruption led to a substitution on male mounting. Interruption was performed similarly for males of both size (GLM; $\chi^2 = 0.252$, df $= 1$, $p = 0.615$).

Female response to male mounting (Online Resource, Figure S4) was recorded in 84% of the mating attempts. Female response to male mounting and mating attempts was strongly correlated ($r = 0.95$, $p < 0.001$). From a total of 87 events of female response to male mating attempt, copulation occurred nearly in 25%; female response to male mounting did not suppress completely copulation (GLM; $\chi^2 = 0.03$, df $= 1$, $p = 0.83$). Males spent on average 48 ± 86 s mounted over a given female in 46 records, but the time a given male remained mounted over a female had no effect over copulation (GLM; $\chi^2 = 2.42$, df $= 1$, $p = 0.11$). Yet, male size significantly affected successful copulation (GLM; $\chi^2 = 4.65$, df $= 1$, $p = 0.03$: Figure 4). Males of bigger size were more successful compared to the smaller size conspecifics. Out of seven recorded copulations, 71% were performed by the male of bigger size.

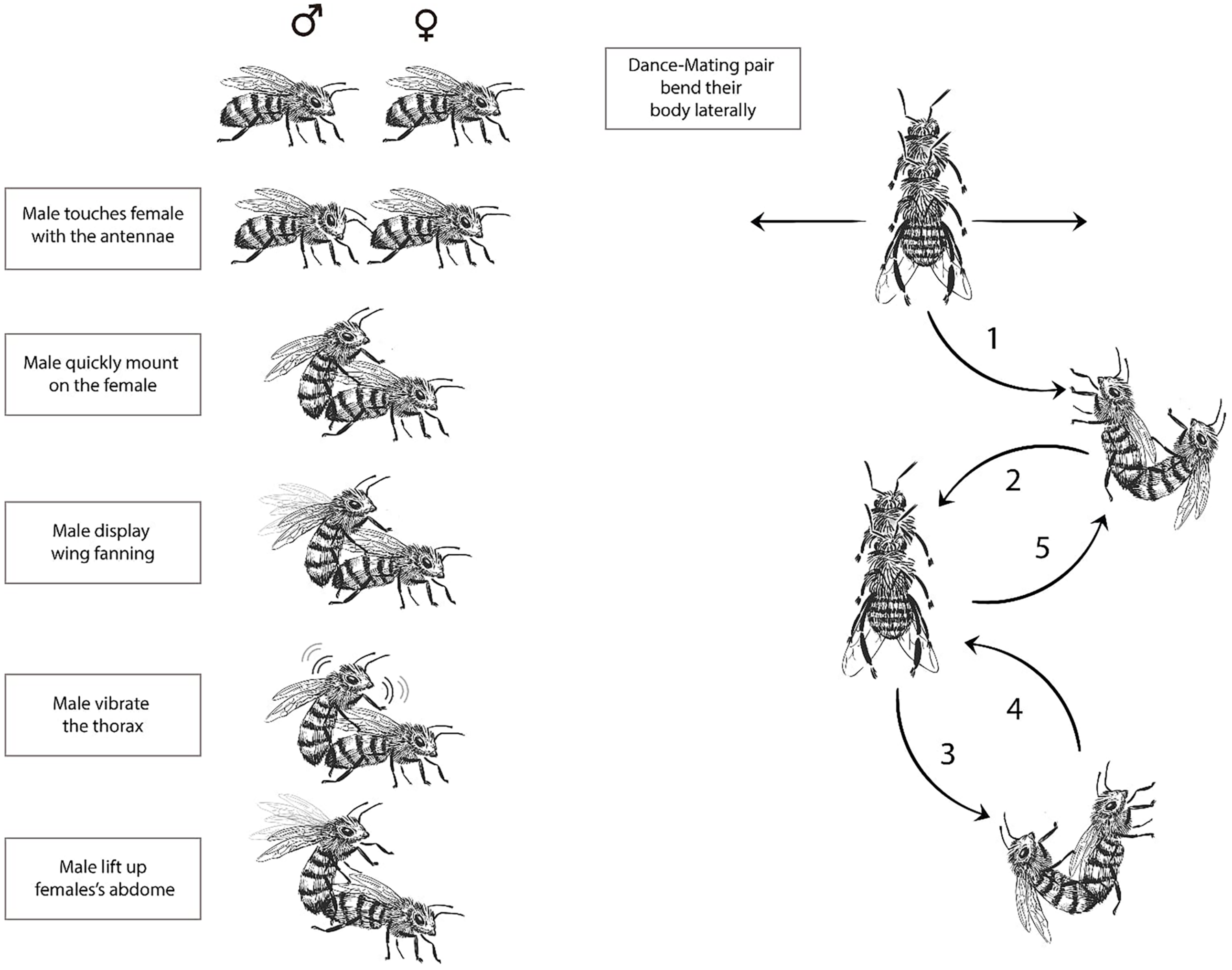


Figure 2. Scheme of pre-copulatory steps and mating in *Heriades truncorum*. Illustration of mating behaviour only for descriptive purposes

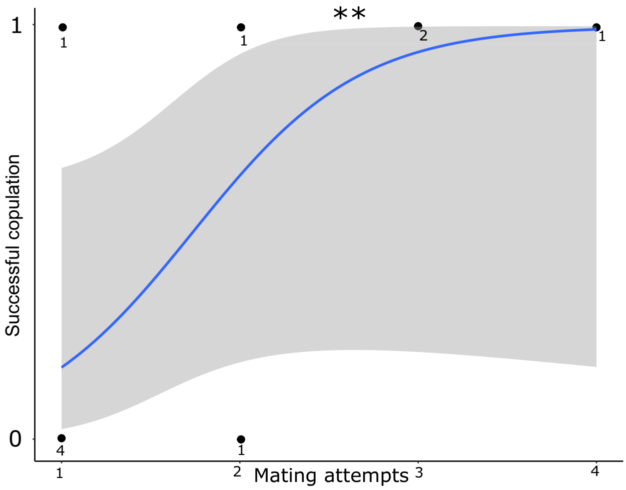


Figure 3. Males of *Heriades truncorum* can perform several matting attempts to successfully copulate. In a mating pair environment (one male for one female), successful copulation increases with mating attempt. Dots and number represent number of observations. Line indicates regression model with 95% confidence interval. $^{**}p<0.05$

Three of these males copulate more than once with the female. Male size alone does not explain higher reproductive success (GLM; $\chi^2=0.90$, df $=1$, $p=0.34$).

4. DISCUSSION

In the current study, I report for the first time the pre-copulatory and aspects of the mating behaviour in *Heriades truncorum*, a small solitary bee oligolectic to Asteraceae species. Males used to display a quick grabbing behaviour after contacting the female's body with its antennae. Once a mating pair is formed, males perform pre-copulatory behaviour including thoracic vibration, wing fanning, lifting female's abdomen and performing sideways rocking movement like a dance. Wing fanning seemed to be a fixed pre-copulatory behaviour. Copulation successes increase with male mating attempts when a male conspecific was absent. Bigger males copulate at higher frequency when a male conspecific was present in the arena. Male reproductive success does not rely necessarily only on male size. Female response to male mounting occurred in 90% of the trials and did not necessarily prevented copulation. Males of both sizes were similarly efficient interrupting mating by separating previously mating partners following replacement. These results support the hypothesis that formation of efficient mating partners relies more strongly on female choice based on male quality with evidence of direct conflict between males independently of their size.

4.1. Courtship display

The males of several bee species display courtship behaviour which might be used by the females as a measure of male quality. Female choice has been shown in solitary bee species, e.g. *Xylocopa varipuncta* (Alcock and Johnson 1990), *Antheronoides micans* (Dutra et al. 2021) and several Megachilidae species such as to *Anthidium maculosum* (Alcock et al. 1977) and *O. bicornis* (Conrad et al. 2010). In well-studied mating system of the Osmiini bee species, *O. bicornis* and *O. cornuta* females are known to use male vibrational signals to measure male quality (Conrad et al. 2010). *Heriades* is related to *Osmia* bee species (Praz et al. 2008), but despite similarities in the use of male vibrational signal (thoracic vibration) and

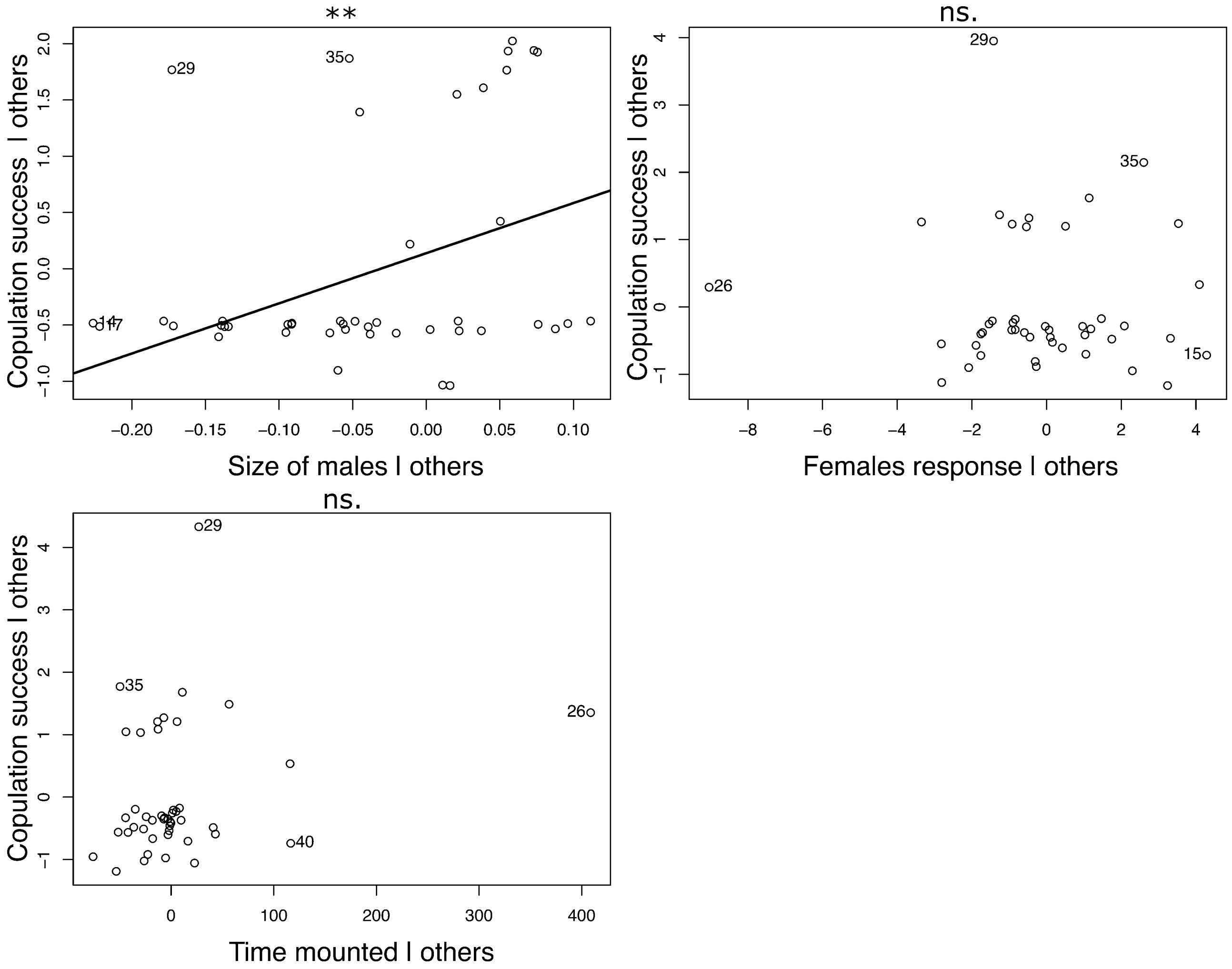


Figure 4. Partial regression plots show the significance of each independent variable (size of males, female response to male mounting and time mounted) over successful copulation. Regression line shown only for significant result. **$p < 0.05$, ns. non-significant

wing fanning, male courtship differs between the two genera. For instance, the wing fanning of males in *O. bicornis* and *O. cornuta* occurs shortly before copulation trials, when males extend its abdomen to reach the female's genitalia chamber (personal observation). Yet in *H. truncorum*, wing fanning takes place as soon as the male mounts over the female. The use of wings seemed to confer to male of *H. truncorum* stability over the females that are often bigger and perform a response to male mounting. Moreover, fanning the wings seems to help males to lift the female's abdomen which anticipates copulation. Lifting the female's abdomen is not exclusively displayed to *H. trucorum*. This behaviour has been observed to occur in *Osmia cornifrons* (Lee et al. 2016), *Megachile willughbiella* (Blochtein, personal communication) and in the cleptoparaiste bee *Nomada lathburiana* (Schindler et al. 2018) as well in non-megachilids such as males of the Neotropical oil bees, *Centris burgdorfi* (Sabino et al. 2017). Although these pre-copulatory behaviours are widely spread across bee species, the current study is limited to account for intraspecific variation (e.g. speed of wing fanning) across populations.

Male thoracic vibration during mating has been recorded to several species (Simmons et al. 2000; Russell et al. 2018; Chiappa and Mandujano 2020; Dec and Vivallo 2021) including other Megachilidae such as *Osmia* spp. (Conrad et al. 2010) and *Megachile* species (Sihag 1986). Interestingly, thoracic vibrations were not mentioned in any of the nine Anthidiini species to which aspects of mating behaviour were investigated (Jaycox 1967; Turell 1976; Alcock et al. 1977; Severinghaus et al. 1981; Frohlich and Parker 1985; Sugiura 1991; Villalobos and Shelly 1991). Yet wing fanning was recorded for members of all three tribes in Megachilidae (Turell 1976; Neff and Simpson 1991; Sugiura 1991; Wittmann and Blochtein 1995; Lee et al. 2016). Ritualized movements are known to be a component of mating systems in some insects. Rocking motions back and forth movement during pre-copulatory behaviour was observed in males of three different species of Anthidini (Turell 1976; Frohlich and Parker 1985). While the sideways rocking movement seems a novelty among the Osminii species, wing fanning, thoracic vibration and sideways rocking movement were registered in *Diadasia rinconis* (Apidae) (Russell et al. 2018).

In Megachilidae species, it has been hypothesized that the pheromone transmission occurs when a male and a female engage in rubbing their antennae together (e.g. *Osmia bicornis*), or males rubbing their front leg tarsus with females' antennae as suggested in *Megachile willughbiella* (Wittmann and Blochtein 1995). Both behaviours were not observed in *H. truncorum*, and this may be explained by the large body size differences between females and males. A potential existence of pheromone and its mechanism of transfer to females remains to be investigated.

4.2. Size of mating partners

Difference in size of males leading to advantage to gather females is mostly reported in species whose males are territorial with pronounced differences in male size (Alcock et al. 1977; Simmons et al. 2000); however, there are exceptions. In *Hoplostilis anthocopoides*, for example, obtention of a territory seems to be independent of size (Eickwort 1977); in *D. rinconis*, a species known to perform scramble competition, bigger males were found to have advantage over smaller ones (Russell et al. 2018). The significant difference in body size between sexes may explain potential scramble competition in *H. truncorum*, as shown by other bees including Osminii bees (Ayasse et al. 2001; Conrad et al. 2010) with apparent advantage for males of bigger sizes in an environment with two males. Since female choice may rely on a size component and as size of individuals reflect their foraging potential and genetic structure (López-Uribe et al. 2019), it would be interesting to investigate, in a natural context, if the effect of environmental stressors leads to inbreeding and population decline due to a potential female choice (relaxation) in regard of male size. Interestingly, in the experiment where no male option was tested, size had no effect, and females mate mostly with males that invested the most in mating by performing several mating attempts. It might show that the size of a mating partner influences female choice when males are not a limited resource and that males of smaller sizes may experience advantage in copulation with low density of bigger size males. Such behavioural choice dynamics, which may rely on additional male traits rather only size as source of quality signals (Ayasse et al. 2001; Benelli et al. 2013), reflect a female plastic behaviour dependent on the density of mating partners (Lehmann 2007; Ribeiro et al. 2010).

Indeed, even with similar number of male mating attempts between environments; in the pair situation, 50% of the trials resulted in copulation, while this percentage raised to 70% in the female choice experiment even with a reduction in observation time (in minutes) compared to the first assay. Furthermore, it was recorded a reduction of nearly 45% of the average time a given male remained mounted over the female in the environment with mating options, suggesting among non-excluding hypothesis: (1) males optimize pre-copulatory quality signals shortening the time of courtship, (2) female choice is quicker. In the environment with competitors, it might be that female quality evaluation may have favoured bigger males during pre-copulatory phase. While further studies of different environment conditions may help to elucidate the factors influencing mating in *H. truncorum*, the current set up shows that female sexual plasticity does not necessarily rely on learning or experience but may have evolved in response to a one-off situation.

Male interference in a mating pair took place in 32% of the observed formation of mating pairs. Males that engage in mating attempt while other males were attached to the female succeed in separating the mating pair. Due to absence of size effect during male interference and lack of aggressive behaviour between males as observed in *Epicharis dejeanni* (Dec and Vivallo 2021), it is more likely that female choice has a stronger effect over selection of a mating partner than in male-male competition. However, it is worth mentioning that experimentally, I did not explore how mating interference occurs among males of extreme body sizes since the frequency of intermediate size males is greater compared to the extreme sizes.

Out of a total of seven copulation events observed in the second experiment, multiple mating, i.e., a female copulating with different males, was observed only once. It is possible that multiple copulations occurred because females may not have been inseminated in the first place. Besides, changes in CHC hydrocarbons, a signal of female reproductive and age status (Thomas 2011; Seidelmann and Rolke 2019), probably require more time than just a few minutes.

4.3. Female response to male mounting

Female resistance to male copulatory attempts is not a novelty in bees. This has been recorded to other Megachilidae species (Severinghaus et al. 1981) and to non-megachilids (Schindler et al. 2018; Dutra et al. 2021). In this study, the females often displayed interactive behaviour as a response to male mounting suggesting that female response functions as a mechanism to evaluate the quality of the mating partner (Parker 2015). Females were observed biting the males' abdomen during the pre-copulatory phase when males were mounted over the female. It was observed that after the female response, the males either released the female or remained performing mating attempts and eventually copulating. This behavioural response has opened several hypotheses regarding its functionality. Here, I tested the hypothesis that females use response to male mounting as a mechanism to evaluate the quality of their mating partners. This behaviour was often recorded but did not completely suppress copulation (negative response); rather, females were observed to stop being aggressive during the pre-copulatory phase and perform mating.

Interestingly, female response also triggered the males to fain their wings. Wing fanning seemed to help males to find suitable positions over the females, and therefore, it might be a mechanism belonging to the complex mating behavioural display of *H. truncorum*. A future experiment preventing the male to fan their wings during pre-copulatory phase would help to elucidate the adaptation of female response to male mounting, male quality and reproductive success in *Heriades truncorum*.

5. CONCLUSIONS

Females display different strategies to evaluate males as potential mating partners. At lower male density, females may copulate more often with males that engaged stronger in mating, while in the environment with higher male density, the size of the mating partner seemed to be of stronger importance to get a mating pair. Engagement on mating can occur simultaneously for multiple males. This behaviour can lead a male to interfere in the copulation of a conspecific.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at https://doi.org/10.1007/s13592-022-00916-7.

ACKNOWLEDGEMENTS

Thanks to Cristina Ganusa for providing the bees and I also thank Ingolf Steffan-Dewenter and Thomas Schmitt for providing the material and lab space. Thanks to Thomas Schmitt, Mark Otieno and John Alcock for commenting in a previous version of the manuscript. Thanks to Maureen Labarussias for the language editing. Thanks to Larissa O. Vilela for providing the mating scheme, to Alan Eriksson for providing the maps and to Taina Conrad for the supportive information. Thanks to Sigmund Collegium for Advanced Studies-University of Würzburg and Aurelia Stiftung for personal support.

AUTHOR CONTRIBUTION

The author confirms sole responsibility for the following study conception and design, data collection, analysis and interpretation of results, and manuscript preparation.

FUNDING

Open Access funding enabled and organized by Projekt DEAL.

DATA AVAILABILITY

Data is available under request.

DECLARATIONS

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The author declares no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

REFERENCES

Alcock J (2009) Animal behavior: An evolutionary approach, 9th ed. Animal behavior: An evolutionary approach, 9th ed.: xvi, 606–xvi, 606.

Alcock J (2013) 45 Advances in the Study of Behavior Sexual selection and the mating behavior of solitary bees. Elsevier Inc., 1–48 pp. https://doi.org/10.1016/B978-0-12-407186-5.00001-X

Alcock J, Johnson MD (1990) Female mate choice in the carpenter bee Xylocopa varipuncta (Hymenoptera: Anthophoridae). Journal of Zoology 221: 195–204. https://doi.org/10.1111/j.1469-7998.1990.tb03991.x

Alcock J, Eickwort GC, Eickwort KR (1977) The reproductive behavior of Anthidium maculosum (Hymenoptera: Megachilidae) and the evolutionary significance of multiple copulations by females. Behavioral Ecology and Sociobiology 2: 385–396. https://doi.org/10.1007/BF00299507

Atwell A, Wagner WE (2014) Female mate choice plasticity is affected by the interaction between male density and female age in a field cricket. Animal

Behaviour 98: 177–183. https://doi.org/10.1016/j.anbehav.2014.10.007

Ayasse M, Paxton RJ, Tengö J (2001) Mating behavior and chemical communication in the order Hymenoptera. Annual Review of Entomology 46: 31–78. https://doi.org/10.1146/annurev.ento.46.1.31

Benelli G, Bonsignori G, Stefanini C, Dario P, Canale A (2013) Male Wing Fanning Performance During Successful and Unsuccessful Mating in the Parasitic Wasp Lariophagus distinguendus Förster (Hymenoptera: Pteromalidae). Journal of Insect Behavior 26: 228–237. https://doi.org/10.1007/s10905-012-9356-2

Chiappa E, Mandujano V (2020) Etograma y análisis de los sonidos realizados por los machos durante la cópula en Colletes musculus (Friese) (Hymenoptera: Colletidae). Revista Chilena De Entomología 46: 553–562. https://doi.org/10.35249/rche.46.4.20.01

Conrad T, Ayasse M (2015) The role of vibrations in population divergence in the red mason bee, *Osmia bicornis*. Current Biology 25: 2819–2822. https://doi.org/10.1016/j.cub.2015.08.059

Conrad T, Paxton RJ, Barth FG, Francke W, Ayasse M (2010) Female choice in the red mason bee, *Osmia rufa* (L.) (Megachilidae). Journal of Experimental Biology 213: 4065–4073. https://doi.org/10.1242/jeb.038174

Dec E, Vivallo F (2021) Reproductive behavior of the oil-collecting bee Epicharis dejeanii (Apidae: Centridini). Apidologie 52: 358–366. https://doi.org/10.1007/s13592-020-00825-7

Dutra AL, Schlindwein C, Oliveira R (2021) Females of a solitary bee reject males to collect food for offspring. Behavioral Ecology 31: 884–891. https://doi.org/10.1093/BEHECO/ARAA026

Eickwort GC (1977) Male territorial behaviour in the mason bee Hoplitis anthocopoides (Hymenoptera: Megachilidae). Animal Behaviour 25: 542–554. https://doi.org/10.1016/0003-3472(77)90105-1

Frohlich DR, Parker FD (1985) Observations on the Nest-building and Reproductive Behavior of a Resin-gathering Bee: Dianthidium ulkei (Hymenoptera: Megachilidae). Annals of the Entomological Society of America 78: 804–810. https://doi.org/10.1093/aesa/78.6.804

Hofmann M, Fleischmann A, Renner S (2020) Foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, inferred from individual tagging, suggest 150 m-rule-of-thumb for flower strip distances. Journal of Hymenoptera Research 77: 105–117. https://doi.org/10.3897/jhr.77.51182.suppl2

Hoikkala A, Aspi J, Suvanto L (1999) Male courtship song frequency as an indicator of male mating success in *Drosophila montana*. Journal of Insect Behavior 12: 599–609. https://doi.org/10.1023/A:1020971518710

Jaycox ER (1967) Territorial Behavior among Males of Anthidium banningense (Hymenoptera : Megachilidae). Journal of the Kansas Entomological Society , 40: 565–570.

Koffler S, Meneses HM, Kleinert ADMP, Jaffé R (2016) Competitive males have higher quality sperm in a monogamous social bee. BMC Evolutionary Biology 16: 1–12. https://doi.org/10.1186/s12862-016-0765-2

Kokko H, Rankin DJ (2006) Lonely hearts or sex in the city? Density-dependent effects in mating systems. Philosophical Transactions of the Royal Society B: Biological Sciences 361: 319–334. https://doi.org/10.1098/rstb.2005.1784

Konzmann S, Kluth M, Karadana D, Lunau K (2020) Pollinator effectiveness of a specialist bee exploiting a generalist plant—tracking pollen transfer by Heriades truncorum with quantum dots. Apidologie 51: 201–211. https://doi.org/10.1007/s13592-019-00700-0

Lee KY, Yoon HJ, Lee KS, Jin BR (2016) Development and mating behavior of Osmia cornifrons (Hymenoptera: Megachilidae) in the constant temperature. Journal of Asia-Pacific Entomology 19: 281–287. https://doi.org/10.1016/j.aspen.2016.03.003

Lehmann GUC (2007) Density-dependent plasticity of sequential mate choice in a bushcricket (Orthoptera: Tettigoniidae). Australian Journal of Zoology 55: 123–130. https://doi.org/10.1071/ZO06105

López-Uribe MM, Jha S, Soro A (2019) A trait-based approach to predict population genetic structure in bees. Molecular Ecology 28: 1919–1929. https://doi.org/10.1111/mec.15028

Maciel de Almeida Correa ML (1981) Contribution a l'étude de la biologie d'*Heriades truncorum* L. (Hymenoptera, Apoidea, Megachilidae). Apidologie 11: 309–339.

Mhatre N, Montealegre-Z F, Balakrishnan R, Robert D (2012) Changing resonator geometry to boost sound power decouples size and song frequency in a small insect. Proceedings of the National Academy of Sciences of the United States of America 109. https://doi.org/10.1073/pnas.1200192109

Michez D, Rasmont P, Terzo M, Vereecken NJ (2019) Bees of Europe. In: N.A.P. (Ed.), Paris.

Neff L, Simpson B (1991) Nest Biology and Mating Behavior of Megachile fortis in Central Texas (Hymenoptera: Megachilidae). Journal of the Kansas entomological Society 64: 324–336.

Parker GA (2015) Reprinted from Bateson (ed .) Mate Choice Printed in Great Britain.

Paxton RJ (2005) Male mating behaviour and mating systems of bees: an overview. Apidologie 36: 145–156.

Praz CJ, Müller A, Danforth BN, Griswold TL, Widmer A, Dorn S (2008) Phylogeny and biogeography of bees of the tribe Osmiini (Hymenoptera: Megachilidae). Molecular Phylogenetics and Evolution 49: 185–197. https://doi.org/10.1016/j.ympev.2008.07.005

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: https://www.r-project.org/.

Ribeiro PD, Daleo P, Iribarne OO (2010) Density affects mating mode and large male mating advantage in a fiddler crab. Oecologia 164: 931–941. https://doi.org/10.1007/s00442-010-1801-3

Rozen JG, Praz CJ (2016) Mature Larvae and Nesting Biologies of Bees Currently Assigned to the Osmiini (Apoidea: Megachilidae). American Museum Novitates 2016-Septe. https://doi.org/10.1206/3864.1

Russell AL, Buchmann SL, De Sabino WO, Papaj DR (2018) Brawls bring buzz: Male Size Influences Competition and Courtship in Diadasia rinconis (Hymenoptera: Apidae). Journal of Insect Science 18: 1–11. https://doi.org/10.1093/jisesa/iey083

Sabino WO, da Silva CI, Alves-dos-Santos I (2017) Mating System and Sleeping Behaviour of the Male and Female Centris (Paracentris) burgdorfi Friese (Apidae, Centridini). Journal of Insect Behavior 30: 103–118. https://doi.org/10.1007/s10905-017-9600-x

Savalli UM, Fox CW (1998) Sexual selection and fitness consequences of male body size in the seed beetle *Stator limatus*. Animal Behaviour 55: 473–483.

Von Schantz T, Göransson G, Andersson G, Fröberg I, Grahn M, Helgée A, Wittzell H (1989) Female choice selects for a viability-based male trait in pheasants. Nature 337: 166–169. https://doi.org/10.1038/337166a0

Schindler M, Hofmann MM, Wittmann D, Renner SS (2018) Courtship behaviour in the genus Nomada - Antennal grabbing and possible transfer of male secretions. Journal of Hymenoptera Research 65: 47–59. https://doi.org/10.3897/jhr.65.24947

Seidelmann K, Rolke D (2019) Advertisement of unreceptivity – Perfume modifications of mason bee females (*Osmia bicornis* and *O. cornuta*) and a non-existing antiaphrodisiac. PLOS ONE 14: e0215925.

Severinghaus LL, Kurtak BH, Eickwort GC (1981) The reproductive behavior of Anthidium manicatum (Hymenoptera: Megachilidae) and the significance of size for territorial males. Behavioral Ecology and Sociobiology 9: 51–58. https://doi.org/10.1007/BF00299853

Shamble PS, Wilgers DJ, Swoboda KA, Hebets EA (2009) Courtship effort is a better predictor of mating success than ornamentation for male wolf spiders. Behavioral Ecology 20: 1242–1251. https://doi.org/10.1093/beheco/arp116

Sihag RC (1986) Reproduction in alfalfa pollinating sub-tropical megachilid bees. 1. Functional anatomy and histology of the organs of reproduction. Zoologischer Anzeiger v. 216.

Simmons LW, Tomkins JL, Alcock J (2000) Can minor males of Dawson's burrowing bee, Amegilla dawsoni (Hymenoptera: Anthophorini) compensate for reduced access to virgin females through sperm competition? Behavioral Ecology 11: 319–325. https://doi.org/10.1093/beheco/11.3.319

Sugiura N (1991) Male territoriality and mating tactics in the wool-carder bee, Anthidium septemspinosum Lepeletier (Hymenoptera: Megachilidae). Journal of Ethology 9: 95–103. https://doi.org/10.1007/BF02350213

Takeshita F, Murai M (2016) The vibrational signals that male fiddler crabs (Uca lactea) use to attract females into their burrows. Science of Nature 103. https://doi.org/10.1007/s00114-016-1371-2

Thomas ML (2011) Detection of female mating status using chemical signals and cues. Biological reviews of the Cambridge Philosophical Society 86: 1–13. https://doi.org/10.1111/j.1469-185X.2010.00130.x

Turell JM (1976) Observations on the mating behavior of Anthidiellum notatum and Anthidiellum perplexum. Journal of the Kansas Entomological Society 59: 55–61.

Vereecken NJ, Mant J, Schiestl FP (2007) Population differentiation in female sex pheromone and male preferences in a solitary bee. Behavioral Ecology and Sociobiology 61: 811–821. https://doi.org/10.1007/s00265-006-0312-z

Villalobos EM, Shelly TE (1991) Correlates of male mating success in two species of Anthidium bees (Hymenoptera : Megachilidae). Behavioral Ecology and Sociobiology 29: 47–53. https://doi.org/10.1007/BF00164294

Wittmann D, Blochtein B (1995) Why males of leafcutter bees hold the females' antennae with their front legs during mating. Apidologie 26: 181–195.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.