



Contents lists available at ScienceDirect

Saudi Journal of Biological Sciences

journal homepage: www.sciencedirect.com

Original article

Mating behaviour and behavioural ecology of a Predatory Wasp, *Symmorphus allobrogus* (de Saussure) (Hymenoptera: Eumeninae)Showket Ahmad Dar^{a,*}, Samy Sayed^b, Mohamed El-Sharnouby^c, Muneer Ahmad Sofi^d, Mudasir Hassan^e, Rizwan Rashid^f, Zahoor Ahmad Dar^g, Sajad Hussain Mir^h, Sayed-Ashraf Elarnaoutyⁱ, Saad H.D. Masry^{j,k}, Ivana Tlak Gajger^{l,*}^a Division of Entomology, KVK- Kargil-II (Zanskar), Ladakh Sher-e-Kashmir University of Agricultural Sciences and Technology of Kashmir, Jammu and Kashmir, India^b Department of Science and Technology, University College-Ranyah, Taif University, B.O. Box 11099, Taif 21944, Saudi Arabia^c Department of Biotechnology, College of Science, Taif University, P.O. Box 11099, Taif 21944, Saudi Arabia^d Department of Entomology, Mountain Research Centre for Field Crops (MRCFC) Khudwani, Sher-e-Kashmir University of Agriculture Sciences and Technology, Jammu and Kashmir, India^e Agriculture Extension Officer, Department of Agriculture, Jammu and Kashmir, India^f Division of Vegetable Science, Sher-e-Kashmir University of Agricultural Sciences and Technology of Kashmir, Shalimar, Srinagar, Jammu and Kashmir, India^g Dryland Agricultural Research Station, Rangreth, Sher-e-Kashmir University of Agricultural Sciences and Technology of Kashmir, Srinagar, Jammu and Kashmir, India^h Department of Entomology, FOA-Wadura Sopore, Sher-e-Kashmir University of Agricultural Sciences and Technology of Kashmir, Srinagar Indiaⁱ Department of Economic Entomology and Pesticides, Faculty of Agriculture, Cairo University, Giza 12613, Egypt^j Department of Plant Protection and Biomolecular Diagnosis, Arid Lands Cultivation Research Institute (ALCRI), City of Scientific Research and Technological Applications, New Borg El-Arab City, P.O. Box 21934 Alexandria, Egypt^k Research and Development Division, ADAFSA, Al Ain, United Arab Emirates^l Department for Biology and Pathology of Fishes and Bees, Faculty of Veterinary Medicine University of Zagreb, Zagreb, Croatia

ARTICLE INFO

Article history:

Received 25 March 2021

Revised 12 April 2021

Accepted 21 April 2021

Available online 30 April 2021

Keywords:

Mating Behaviour

Behavioural Ecology

Predatory Wasp

Symmorphus allobrogus

ABSTRACT

This paper represents an attempt to investigate the mating behaviour of *Symmorphus allobrogus*, explaining the willingness of male to mount and copulate. The male displays including mode and frequency of antennation and position while copulating, the displays further comprises of intensity and frequency of rejecting behaviour. The presence of the male's copulatory and postcopulatory courtship studies, understands the maintenance of monandry. The wasp has numerous secondary sexual characters, and the mating behaviour follows a phyletic and the specific sexual mating characters in context of sexual selection. The duration of mating phases and the number of male antennation series during precopulatory, copulatory and postcopulatory phases of mounting, differs significantly. Mating success depends mostly on the activities of male in the premounting phase and the behaviour of both sexes has a roughly equal importance for it in precopulatory phase. While during copulation, activity of male has little influence on its duration; however, behaviour of female has crucial effect, inducing its earlier termination.

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Peer review under responsibility of King Saud University.



Production and hosting by Elsevier

1. Introduction

Eumeninae is the most diverse group, with 3,579 species in world (Pickett and Carpenter, 2010), among this there are only 19 species of the genus *Symmorphus* (Li and Chen, 2014) known, which act as predator of chrysomelidae beetle. Diseases and parasites are common in economically important insects (Tlak Gajger et al, 2020; Tlak Gajger et al, 2014a; Tlak Gajger et al, 2010). The stinging pattern of *Symmorphus* species to beetle includes regular stings to throat, three thoracic and the first abdominal segment, therefore it is an important biocontrol agent. Mating behaviour demonstrate the different aspects and steps of ethological evolution in the wasps. But the male dominated mating characteristics

<https://doi.org/10.1016/j.sjbs.2021.04.078>

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such as courtship and pre and post copulatory behaviour of most of eumeninae wasp species viz. *Symmorphus allobrogus* (de Saussure); *Symmorphus bifasciatus* (Linnaeus), *Symmorphus crassicornis* (Panzer), *Symmorphus murarius* (Linnaeus); *Ancistrocerus antilope* (Panzer), *Ancistrocerus trifasciatus* (Müller), *Discoelius dufourii* (Lepeletier), and *Discoelius zonalis* (Panzer) were not known in detail. Mate choice has long been appreciated as a key component of sexual selection (Dougherty and Shukar, 2014). The reproductive success may be affected by pre-mating events, resulting in male and female choice, as well as postmating events, including male-male competition in the form of sperm competition and cryptic female choice. Males of many wasps in the subfamily Eumeninae have numerous secondary sexual characters, which provide much systematic information. In *Linnaeidea distinguendus* male mating success was affected by the quality of the wing fanning in the courtship phase (Giovanni et al., 2013). Studies of mating behaviour before, during and after copulation provide explanations for the diversity and evolution of mating systems, patterns of mate guarding and sperm competition (Alcock, 1994), or adaptations of copulatory mechanisms in groups of closely relative species (Miller, 2003). Similarly, copulation is the result of various interacting factors, including female reproductive status, male courtship behaviour like approach and antennation (Boake et al., 2000), visual and chemical cues (Canale et al., 2012), male choice, female responses to courtship and female choice like active posture and wing vibration, mutual mate choice like aggression and antennation (Boughman, 2002) and in *Chorthippus biguttulus* males acoustic courtship signals are evaluated by females for mate choice (Wittmann et al., 2011). In fruit fly's male-male courtship is prevalent (Dukas, 2010), while as, in *Psytalia concolor* it depends upon the mate location (Canale et al., 2012). Within Eumeninae, the sexual selection results in diversity with regard to behaviour and structures used by males during courtship, duration of single copulation, repeated copulations by a single pair of wasps, and post-insemination displays (Cowan, 1991). Till that no work on any aspect regarding to this wasp species have been done in India. Therefore, this paper is a preliminary work aimed at studying the behaviour elements as well as individual parameters related to mating success of *S. allobrogus* in temperate conditions of Kashmir valley.

2. Materials and Methods

The field research was carried out in Kashmir valley (India) during 2013 and 2014 in the six biodiversity rich localities situated at 1500, 1650, 1800, 2432, 4800 and 5100 meters above sea level (ASL). In Kashmir the *S. allobrogus* species is most common and act as model for the mating studies. The males and females were collected from all study sites during spring season and identified in the laboratory. For mating observations during 2014, the wasps were kept in groups of one sex in plastic cages at the room temperature of 23 to 25 °C, with *ad libitum* available food. The age of wasps used in experiments varied between newly emerged to 47 days for females and up to 43 days for males. During the present investigation the collected larvae were kept in laboratory under controlled conditions. Previously parallel study was conducted by Budrine and Budrys (2004) and Cowan (1986) on various species of this wasp.

2.1. Mating experiment

Male and female pairings was observed in an arena with a diameter of 23 cm under a bell-glass of 22 cm height maintained at constant temperature of 22 to 29 °C, with white thick paper cover outside. The bell-glass was exposed to the daylight, with

additional artificial bright tube light illumination for three to four hours. A single virgin female was placed under the bell-glass in the cage with a single male was situated near the latter and allowed a 1 to 5 min acclimation period. The several mating trials were monitored continuously for 2 h after acclimation period, and numbers of mating attempts performed by each male were recorded until dismounting takes place. Copulating pairs were left in the perforated plastic cages provided with sensitive perching paper surface and were observed every 10 min until they separated naturally, or until 6 h after the mating trial when they were separated manually. Some females were used up to ten times to investigate their willingness to mate; the males were used between one and twelve times. In order to prevent wasps from responding to odour cues left by previous pairings. The paper layer was cleared by alcohol solution between the successive trials and changed after each mounting.

2.2. Mounting

It involves four to five successive mounting struggles in arena which are measured with respect to the time period during which the particular event like; pre-mounting phase or courtship, mounting phase, post-copulatory phase (termination of copulation), copulatory phase (intromitting to extraction of genitalia), post copulatory (termination of copulation), and post mounting phases have occurred.

2.3. Mating behaviour elements

We categorized the observed actions into different mating behaviour elements, 54% of which were characteristics of both sexes and 30.77% by males and 15.38% by females (Table 2). Mating behavioural elements was quantified using the frequency of the particular event. Total number of recorded actions was divided by the duration (in minutes) of corresponding mating phase. Mating success was analyzed regarding the individual parameters and behaviour elements of mates as an independent variable. The dependent variable *i.e.* mating success was estimated by presence/absence of mounting, copulation and duration of copulation. Significance of difference in individual parameters and frequency of elements in successful and unsuccessful mating was estimated applying the Mann-Whitney *U* test. The dependence of the individual parameters and behaviour elements in mating success including the pre-mounting and precopulatory phases was analyzed using non-parametric Kendall Tau Correlation and the interaction was assessed using logistic regression.

2.4. Remating experiments

During remating experiments, we investigate that whether studied Eumeninae wasp species is facultative polyandrous, therefore, we tested eight previously mated females of *S. allobrogus*. Each inseminated (mated) female was allowed to try to pair with one male once per day. Out of 23 trials of remating 2, 3 and 4 females were paired during 4th, 3rd and 2nd subsequent days, respectively. As the inseminated females always rejected the males that were vigorous and attempted to copulate.

3. Results and Discussion

3.1. Mating behaviour and behavioural ecology

In laboratory conditions males emerged 2 days earlier than females, similarly to previously published data (Sultana and Wagan, 2008) and they were active for about 4 weeks. Males spent

much time at nesting sites waiting and searching for receptive females. Wasp male's choice may often occur under a variety of circumstances and involves a series of activities. The results of present (Table 2) investigation exhibited that the activities of *S. allobrogus* male comprises patrolling the nest aggregations, locating a cavity with a female, touching conspecific foraging females, brief pouncing on conspecific males as well as dark objects of similar shape and size. Although, in insects sometimes there is possibility of activities of mutual mate choice (Fritzsche and Arnqvist, 2011). Copulations of *S. allobrogus* is never observed at the nesting site. The mating period was short and majority of copulations occurred during the first day after female's emergence, although female start nesting activities 4 to 5 days earlier, generally involve a much greater investment than those of males. No males of the other wasp species were ever seen at the nest aggregation site. Wasps visiting the patch of suitable inflorescences in search for conspecific females are known for *Ancistrocerus antilope* (Cowan and Waldbauer, 1984). Results showed that mating strategy and mating site choice depends on the ecological and behavioural variables that include population density as well as female mating frequency. High population density and low female mating frequency stimulate the patrolling of female emergence sites, whereas low population density may determine other mating tactics as the sexual selection is largely driven by the availability of mates (Tinghitella et al., 2015). The mating system of *S. allobrogus* can be classified as one of scramble competition polygyny, when the occurrence of females is focused in space and time, males do not compete with each other directly by defending territories or resources but by a race for receptive females, as the ability to locate females being of great importance for mating success. The male interactions are minimal in extremely low-density populations, as density increases, male's exhibit territoriality (Kwiatkowski and Sullivan, 2002).

3.2. Mating phases and activities in captivity

In present experiment out of total 165 pairings in populations of *S. allobrogus* only 67% (110 pairs) resulted in mountings ($df = 1 > 4$, $2, P < 0.05$) and only 60% (66 pairs) of mountings resulted in the successful copulation. This difference may reflect intrinsic higher choosiness of mates, and a male took a horizontal position over a female on her dorsum with head above head. In nearly 3.5% (5.77 pairs of 165 pairings) of all mountings the male initially mounted the female in antiparallel position. He started to attenuates her abdominal tip but after few seconds of such behaviour, always returned to a typical position. This behaviour occurred in virgin males as well as those having earlier mating experience, thus we may conclude that it does not depend on the male's experience; however, no such observation as an indication of mating willingness were recorded in females. When mounted, males buzzed their wings and held their mouthparts on females' pronotum or vertex, at the area of the cephalic foveae. Males held their forelegs around the sides of females' pronotum, mid legs on the sides of her propodeum, and hind legs close to her petiole. In investigation the antennation of female antennae was one of the behaviour elements of male which is distinctive to each species. Males use mostly the tactile cues in mate recognition as a courtship behaviour; as indicated by observations of male touching of female antennae, elytra and pronotum with their antennae during courtship, same were observed in hymenoptera by Sakurai et al. (2011). Further, the copulation in insects is influenced by age and sexual maturity of mates, tactile and chemical cues (Tinzaara et al., 2011), reproductive status of mates (Carazo et al., 2004), male courtship behaviour (Boake et al., 2000), female responses to courtship (Edvardsson and Arnqvist, 2000), and mate choice (Salehialavi et al., 2011) and, to some extent, mate choice (Perry

and Rowe, 2010) influence the occurrence of precopulatory behaviour during mating. The stroking is species specific and involves the jerking motion in *S. allobrogus*. Males of *S. allobrogus* demonstrated a close number of precopulatory antennal strokings (about 4 times on average). While antennation, males placed their antennae between those of females, started to stroke regularly the females' antennae from pedicel to flagellum, and probed with their genitalia from the side towards the tip of females' metasoma. During this stroking, the ventrolateral side of the male's antennae having 8 to 11 flagellomeres, contacted with the dorsolateral side of the females' antennae. Mating duration and the number of strokes were higher in unmated males than in mated ones, and removal of male antennae and obscurity of elytral patterns significantly decreased mating success. However, in *Anegleis cardoni*, female antennal ablation and obscuring of the pronotum did not affect mate recognition (Omkar et al., 2013). As soon as males mounted, some females initiated struggling behaviour consisting of erecting or lowering their antennae and concealing them under their deflected heads, curling their metasomata forward ventrally or sometimes rotating their mesosomata around their longitudinal axis. From the above observations only 67% of all trials resulted in mountings implies presence of willing mates and the males which demonstrated close numbers of precopulatory antennal strokings to opposite mate that stimulate for successful copulation.

3.3. Activities after copulation

The *S. allobrogus* male and female remained together for the period ranged from 3 to 790 sec, after the termination of copulation. However, in general, wasp male and female usually separated immediately after copulation (Budriene, 2004). The young males simply rode the females, but in four events lasting for 29 to 548 sec, males-initiated courtship behaviour that is known to be influenced by age and sexual maturity of mates, same were recorded by Tinzaara et al. (2011). Occurrences of the postcopulatory phase in *S. allobrogus* last for only 3.9 sec. Since sperm displacement in monandrous *S. allobrogus* is not an issue, the adaptive function of post-copulatory riding is unclear. Possible role of this behaviour in wasps is to signal a successful copulation. The postcopulatory phase is associated with the series of antennations lasting for fraction of seconds ($N = 62$, $X = 0.14$). Regular occurrence of postcopulatory behaviour in some species, like *S. crassicornis*, may alternatively suggest that they are facultative polyandrous (Budriene, 2004). Remating an activity observed to less extent in the *S. allobrogus* occurs after the copulation is over and has significance to determine and prove the monandrous nature of the species. For instance, in parasitoid wasp *Aphytis melinus*, female was previously thought to be unreceptive after their first mating, guarding and associated post copulatory behaviour of male helped to 'switch off' female's receptivity as well as reduced the proportion of progeny sired by the second mating male (Allen et al., 1994). In *Cotesia rubecula* most females mate only once, however, courting rival males frequently approach mating pairs, and expectedly there is a brief time window after the first mating when they would accept a second mate (Field and Keller, 1993).

3.4. Duration of mating phases

Thus, in captivity male and female spent more time period to find each other. Mean duration of precopulatory phase of mounting lasted >99 sec (1.65 min), (Table 1) follows the successful courtship sometimes lasts for more than this period. In parasitic wasp, *Psytalia concolor* immature males do not appear to gain from receiving male courtship, but they develop a higher intensity in shorter latency time (Giovanni and Angelo, 2012). It supports the resulted variability of mean copulatory period of *S. allobrogus*. Budriene

Table 1
Activities of reproductive behaviour of *Symmorphus allobrogus* – average duration.

Mating Value (Mean ± SE) of the character	Time in seconds
Duration of pre-mounting phase following successful mounting	899 ± 79
Duration of precopulatory (“courtship”) phase following successful copulation	99 ± 85
Duration of copulation (seconds)	76 ± 45
Duration of postcopulatory phase (“mate guarding”) (seconds)	3.9 ± 39
Duration of copulation after dismounting (“falling backward”)	2.21 ± 0.99
Number of antennation series in the precopulatory phase	4.9 ± 0.38
Number of antennation series in the copulation phase	0.78 ± 0.12
Number of antennation series in the postcopulatory phase	0.14 ± 0.08

N = 165 pairing, N = 176 behavioral activities; P < 0.05.

(2004) confirmed that on an average *S. allobrogus* mounted later than the other species. Further, mating duration and the number of strokes were higher in unmated males than in mated ones (Omkar et al., 2013). The regression analysis of time duration (S) of reproductive activity and behaviour gives the multiple regression coefficient (R) of 0.99, R² equal to 0.99 and the standard error of 3.22.

3.5. Morphological structures involved in mating behavior

Female’s struggling during precopulatory, premounting or copulatory period may suggest the existence of direct or “cryptic” female choice (Table 2), with sexual selection acting on male’s behaviours and morphological structures used during this period. The males of species stroked females’ antennae using their modified apical flagellomeres, often bearing convex plates of species-specific structure, called tyloids, during the courtship and copulation. The web-building spider generates a distinct vibratory signal that delays female aggression during the courtship. Probably, the male antennation provides the female with tactile information about the con-specificity and status of the male. In several observations, a drop of bright yellow liquid excretion appeared on apical segments (Flagomere) of male antenna. As soon as the male began antennating the female, the drop was gradually reduced perhaps because of its spreading over surface of her antenna. This visible antennal excretion was observed in six mating trials of *S. allobrogus* (in 5% of all mountings; four of them resulted in copulation). The, large amount of the antennal excretion is likely to be associated with the mating status (i.e., virginity or age) of male. While as, in case of *Argiope keyserlingi* males’ shudder by quickly rocking

Table 2
Mating behaviour elements of the solitary wasp *Symmorphus allobrogus* - average frequency

Behavioural element	Mating	Mating phase and frequency of the element (actions/min. Mean ± SE).
Aggression	Both	Premounting: female 0.065 ± 0.006, male 0.0017 ± 0.0004
Approach	Both	Premounting: female 0.074 ± 0.005, male 0.124 ± 0.008
Abdomen extending	Both	Premounting: female 0.0003 ± 0.0002, male 0.011 ± 0.001
Falling backwards	Male	Copulation: 0.36 ± 0.03
Jump	Both	Premounting: female 0.026 ± 0.006, male 0.055 ± 0.006
Mate antenna antennation	Male	Precopulatory: 3.85 ± 0.15; copulation: 0.74 ± 0.06
Moving back	Male	Precopulatory: 0.003 ± 0.002; copulation: 0.020 ± 0.007
Shaking	Female	Precopulatory: 0.71 ± 0.06; copulation: 0.27 ± 0
Struggle	Female	precopulatory: 1.1; copulation: 0.7 ± 0.03; Premounting: 0.0007;
Plopping	Both	Premounting: female 0.028 ± 0.006, male 0.022 ± 0.003
Abdominal stroking	Male	Precopulatory: 2.80 ± 0.1
Antennation	Both	Premounting: female 0.013 ± 0.002, male 0.069 ± 0.005
Wing vibration	Both	Premounting: female 0.0014 ± 0.0005, male 0.0042 ± 0.0008; precopulatory: male 0.06 ± 0.01; copulation: male 0.014 ± 0.005

N = 165 Pairing; N = 110 premounting; N = 66 copulation, statistically significant, p < 0.05.

anterior to posterior in the web several times, a sort of movement that generates a distinct vibration in the female’s web, a form of ‘tremulation’ signal, that (Shudder) reduces the female’s aggression (Uhl and Elias, 2011). Thus, we hypothesize that while antennation of the male, the female receives not only tactile but also specific chemical information (contact pheromone) about his con-specificity and status. The studies of antennal tyloids of the male parasitoid wasp *Pimpla turionella* (L.) (Bin et al. 1999) support our observations. It was revealed that tyloids of *Pimpla* release the chemical structures of integumentary glands rather than sensory organs. Behavioural observations of mating in *P. turionella* indicate that the intensity of antennal stroking is dependent on female receptiveness, as the antennation of female’s antennae is an important determinant of the copulation success, in this context we may suggest that the tyloids of *S. allobrogus* have a similar excretory function and serve as a source of contact pheromones while mating. The cephalic foveae, depressions on vertex behind the posterior ocelli of females of *S. allobrogus* represent an external opening of integumentary glands that play a role in mating. Typically, a mounted male holds his mouthparts close to the vertex of the female, thus the excretions from the foveae may affect sensilla of his mandibles and palpi. Thereby, enable the male to recognize female species receptiveness by touching or prodding her vertex.

The information on the functions of cephalic foveae in wasp is very scarce; however, it needs further investigation. The mounted male of the *S. allobrogus* species grasped the sides of female’s mesosoma, touching her pronotum, mesopleuron, propodeum, and petiole or the second metasomal tergite with his legs. In addition to holding mouthparts on the vertex of the female, male also often placed them on her pronotum. He appeared to test on sculpture of cuticle, using his antennae, palpi and tarsi, to test whether the mate is conspecific and of the right sex. Therefore, the species-specific structure and sculpture of cuticle of these body parts is not only used for recognition of mate by the wasps, but it is an important morphological character in taxonomy, used for identification of wasp species.

3.6. Behavioral elements that influence mating success

The mating success studied for *S. allobrogus*, involves 66 successful mating observations in the laboratory. In general, there is a significant difference in the mating success between field and laboratory conditions. In small laboratory cages: average of 22.37% of 295 taken (40% of total being mounted by male) of females were inseminated, no matter the treatment, the age of males, and the sex ratio. However, in contrast *Aedes aegypti* female

Table 3Effect of frequency of mating elements in precopulatory (courtship) phases on mating success of *Symmorphus allobrogus* (N = 110; dependent variable; presence of copulation).

Behaviour elements (acts/min.)	Correlation/ Kendall t	Logistic regression	Mating possibility
Female's actions			
Aggression*	−0.15	n/s	–
Alert posture	0.07	0.06 ± 0.01	Yes
Approach*	−0.13	n/s	–
Jump	−0.05	n/s	–
Wing vibration	−0.05	n/s	–
Males behaviour			
Aggression*	−0.14	−17.4 ± 6.2	–
Alert posture	−0.14	−12.2 ± 6.2	–
Approach	0.08	0.09 ± 0.01	Yes (high)
Substrate antennation	0.10	0.06 ± 0.02	Yes (high)
Abdomen extending	n/s	8.6 ± 3.2	Yes
	Intercept (b ⁰ correct predictions)	S 68.9%	

Highly significant values, having $P < 0.001$, in bold; n/s-non-significant ($P > 0.05$).

insemination rates in high population density of small cages of size 0.009 m × 0.01 m were 81.6–98.7% as compared with 65.4–84.6% in large low-density laboratory cage of size 9 m × 15 m under field conditions (Ponlawat and Harrington, 2009). Table 3, represents the observed mating behaviour elements and their average frequency. As *S. allobrogus* females seem to be monandrous, whereas males can copulate multiple times. The study of the influence of the behaviour elements of the premounting and precopulatory phases on mating success revealed significant relationship part of which were confirmed by the logistic regression analysis. Results showed that female alert posture, male approach, antennation and abdomen extension during the mating are important for successful courtship; while as, several other factors were statistically non-significant and weakly associated with the mating to occur.

3.7. Premounting period

This phase includes: approach, aggression, examine, jump, abdomen extending and wing vibration. The probability of mounting negatively correlated with the frequency of female approach and aggression to the male, although the average frequency of these behaviour elements was slightly higher in successful mating experiments than in those without mounting, same observations were recorded by Omkar et al. (2013) while studying the mating behaviour of *Anegleis cardoni*. Further, the attempts to mount of an active and finally successful male caused stronger aggressive behaviour of the female that possibly reflected its direct assessment of male. The positive effect of female's jumps possibly shows that active females are easier detected by males and suggests the importance of visual cues in the premounting phase of mating behaviour of *S. allobrogus*. The success of the males in mounting is more than > 60% of all observations, the male's extending of abdomen may give visual cues for the con-specific mate recognition by the female, thus increasing the probability of mating success. Workers of several species of neotropical wasps hold the distal tip of their colourfull abdomen stretched erect while colony defence, which is accompanied by various combinations of wing fanning, waving of the gaster, and extrusion of the sting (O'Donnell et al., 1997), thus leads to the mounting by males. Male's abdomen extending behaviour has a communicative function to nest mates when wing fanning in conjunction with gaster flagging may volatilise and disperse alarm pheromones from venom or from other exocrine sources. During daily patrols, male stenogastrine wasps display three white stripes on their tergites by fully stretching their abdomen, behaviour leads to gaster flagging, a signal for mounting. Furthermore, in *Parischnogaster mellyi*, a positive relationship between mating and abdomen extending display frequency of males was found (Beani and Turilazzi,

1999). The alert posture or aggressive behaviour of the male had the strongest negative correlation with mating success; this was confirmed by the logistic regression analysis (Table 3) as well as the comparison of average frequency in successful and unsuccessful mating experiments.

3.8. Precopulatory period

Precopulatory behaviour of both sexes had influence on mating success, nearly 60% were exhibited by males and 40% by females (Table 2). Vigorous struggle of the female had a negative influence on copulation, while slower shaking affected it positively. Female alert posture ($r = 0.06 \pm 0.01$; $t = 0.07$) was found to lead successful mating but the reason was possibly the release of the high concentration of attracting cues which trigger the male to mate, but same was not found in case of the male alert posture behavioral element. Similarly, the female approach and jump give mostly non-significant results as shown by regression analysis (Table 2). In *Lariophagus distinguendus* after the female perception of males and during mating attempts, fanning before a successful courtship differed compared to wing fanning performed prior to an unsuccessful courtship in terms of their mean frequency and time period, but not their amplitude (Benelli et al., 2013). Therefore, we may expect some sort of female's choice at this phase: it is possible that the female uses the rejection response as an exercise of mate's assessment. Mating systems of some insects such as flies and water striders involve a premating vigorous struggle that results in the rejection of undesirable males as well (Sih et al., 2002). The most important activities of the male, stimulating the female to copulate, were antennation involving the stroking of female's antennae by the tyloidea and stroking by abdomen and the approach.

The male tyloids function as integumentary gland, releasing contact pheromones inducing readiness of female to copulate. Firstly, *S. allobrogus* female recognition by males mediated by a volatile sex pheromone, triggers the behavioural sequence leading to mounting, and secondly, the female recognizes and accepts the male after antennal contact ($r = 0.06 \pm 0.02$) that in turn is mediated by the secretion from the male antennal glands, which acts as a contact pheromone.

3.9. Copulatory period

In the copulatory phase, the activities of the female have the major role, significantly affecting the duration of copulation through shaking and vigorous struggle. Remarkably, antennation of the male was less frequent than in the precopulatory phase but still active; however, it did not significantly affect the duration of copulation in *S. allobrogus*.

3.10. Remating

Uhl et al. (2015) demonstrated that in spider the mating while mounting clearly prevents the female from exerting the control over mating frequency and duration and the female may be monopolized by male against her interest, constituting the sexual conflict. However, males of *S. allobrogus* (110 pairs; 67% of all test trials) showed high frequencies of mounting being almost the same as those for virgin females of *S. allobrogus*. Our results suggest that visual cues do the most important determinant of mounting decisions as also confirmed by (Budriene and Budrys, 2012). Observations of mating cues may have been involved in male recognition of female mating status after the mounting have occurred. The rate of female remating can have important impacts on a species, affecting the cooperation within families, to population viability and gene flow (Fisher et al., 2013). Although female remating has been studied extensively in insects. Second male mating has a negative latitudinal cline opposite to that of first mating, as the latency and copulation period differ significantly between first and second male mating experiments in *Drosophila melanogaster* (Chahal et al., 2013). On the other hand, females of *D. melanogaster* adapted to one environment tended to produce a higher proportion of offspring sired by their first mate as compared to second mating when adapted in other environment, suggesting ecologically based divergence of this conflict phenotype (Arbuthnott et al., 2014). However, in the present investigation no ecological factors were observed to affect the remating conflict of *S. allobrogus*. Female remating rate is extremely variable, ranging from females mating with a single male in their lifetime, to extreme polyandry where a female may mate with hundreds of males. About 77% of females reject remating and the majority (23%) of all rematings occurred only when the female failed to produce offspring from her first mating (Fisher et al., 2013).

4. Conclusion

The work conducted in temperate areas of Kashmir region represents an attempt to investigate the mating behaviour of *S. allobrogus*. The wasp has numerous secondary sexual characters, and the mating behaviour follows a phyletic and the specific sexual mating characters in context of sexual selection.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank to DST, New Delhi, India for providing the financial assistance to conduct this study. Further, the thanks are also to SKUAST-Kashmir, Srinagar for providing computer and internet facilities and to the All India coordinated research project on pollinators and pollinizers, (AICPP) SKUAST-K, for assisting in identification availing me the laboratory facilities. This work was funded by Taif University Researches Supporting Project number (TURSP-2020/139), Taif University, Taif, Saudi Arabia.

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