Antennation and sexual performance of male digger wasps
*Sphex ingens* Smith (Hymenoptera: Sphecidae)

C.A.S. Souza\(^a,b\), F. Prezoto\(^a\), M.S.C.S. Lima\(^c\) and J. Pederassi\(^d\)

\(^a\)Programa de Pós-Graduação em Ciências Biológicas (Comportamento e Biologia Animal), Laboratório de Ecologia Comportamental e Bioacústica (LABEC), Universidade Federal de Juiz de Fora (UFJF), campus Universitário Martelos, Juiz de Fora, Brazil; \(^b\)Centro Universitário de Barra Mansa (UBM), campus Barra Mansa, Barra Mansa, Brazil; \(^c\)Departamento de Zoologia, Universidade Federal do Piauí (UFPI), campus Amilcar Ferreira Sobral, Floriano, Brazil; \(^d\)Departamento de Vertebrados, Museu Nacional, Universidade Federal do Rio de Janeiro (UFRJ), Rio de Janeiro, Brazil

**ABSTRACT**

Antennation can play several roles in hymenopteran copulation, mainly in wasps. The digger wasp *Sphex ingens* Smith has a very peculiar sexual behaviour, in which forced copulation is a striking element. However, communication through antennation during the pre-copulation and copulation phases and the relationship between the sexual performance of males and the final result of copulation require further clarification. The sexual behaviour of wild populations of *S. ingens* was filmed during the breeding season in a site between the beaches Meros and Aventureiro, Ilha Grande, southeastern Brazil. We assessed antennation behaviour, courtship duration, sexual performance, and genital clasping. Only successful males had the genital clasping assessed. Evidence found so far points out that the successful males showed better sexual performance – that is, they antennated more in a shorter courtship duration. Also, genital clasping in successful males did not depend on antennation, courtship duration, or sexual performance. Our results shed light on some aspects of the sexual behaviour of wasps, as they explain part of the sexual selection mechanisms adopted by the species.

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**Introduction**

Hymenopterans represent the apex of courtship behaviour, as they have the most diversified repertoire among insects (Dethier and Stellar 1970). In several hymenopteran species, the movements of legs or mouth parts, wing fanning, or antennation are important stimuli for the assessment of female receptivity to maximise copulation success (Barass 1960, 1961; Leonard and Ringo 1978; Tagawa et al. 1985; Kainoh 1986; Martins 1993; van den Assem and Werren 1994; Pimenta and Martins 1999; Guerrieri et al. 2001; Romani et al. 2003, 2005; Cheng et al. 2004).

In general, male spheciform wasps increase their reproductive success by using strategies (e.g. patrolling, territorialism and nest guards) and adaptive specialisations
(e.g. body size and secretion of substances) (Evans 1966; Alcock 1975; Chiappa 1996; Herzner et al. 2003; Alcock and Kemp 2005; Kroiss et al. 2010). However, the courtship behaviour of wasps is still poorly known in terms of successful or unsuccessful copulations.

The digger wasp *Sphex ingens* Smith is a large sphecid (Bohart and Menke 1976) that occurs in Brazil in the states of Bahia, Espírito Santo, Rio de Janeiro and São Paulo (Amarante 2002).

Promiscuous mating and forced and multiple copulations are fundamental elements of the sexual behaviour of *S. ingens*. In addition, its behavioural repertoire is characterised by a different time investment among mating phases. Antennation was the most frequently observed behaviour and was restricted to the pre-copulation and copulation phases (see Souza et al. 2015).

However, Souza et al. (2015), based on a probabilistic model, suggested that the antennation behaviour observed in males does not affect *S. ingens* mating. In particular, the copulation success (or mate selection) is not affected, as the results of the transition of agonistic behaviours in females were the most significant (i.e. escalating aggressiveness, aggressive display, confrontation and drumming).

Hence, evidence about antennation behaviour and its relationship with copulation outcome is so strong that it cannot be overlooked. This evidence raises the following questions: (1) Do successful copulating males antennate more frequently during courtship than unsuccessful males? and (2) Does antennation during courtship influence copulation outcome in *S. ingens*? In this context, the present study aimed at investigating the role of antennation in the courtship of *S. ingens* and its relationship with sexual performance, in order to understand the role and adaptive value of this behaviour in *S. ingens*.

### Material and methods

#### Study area and data collection

Nesting sites were found above foredune areas on the beaches Meros (Praia do Sul State Biological Reserve – RBEPS: 23°13′7.35″S, 44°20′21.14″W) and Aventureiro (Aventureiro Sustainable Development Reserve – RDSA: 23°11′21.67″S, 44°19′7.73″W), Ilha Grande, southeastern Brazil, the latter located between the houses of local families. The study was carried out during the first and second fortnights of January 2011 and comprised a total sampling effort of 32 h.

We captured and marked with non-toxic paint males and females found in nesting sites (Martins 1993), and then released them. We recorded their repertoire of copulation behaviours using a digital camcorder and a chronometer. In a video-editing lab, the videos were digitally analysed for the selection of parts of interest.

We analysed only the couples undergoing the pre-copulation and copulation phases (Souza et al. 2015). We assessed the influence of antennation on the sexual performance of males in complete copulation attempts (from the intromission of the aedeagus and the practice of the connubium, regardless of copulation outcome – successful or unsuccessful). Therefore, we considered the following variables: (1) antennation – number of times that the antennae touched the female during courtship in a copulation attempt; (2) courtship duration – total time invested in a copulation attempt, mediated by antennation behaviour; this variable is necessary to measure success frequency (successful
copulations) and total duration of mating of the males monitored between the pre-
copulation and copulation phases; (3) sexual performance – coefficient obtained by the
division of antennation by courtship duration; and (4) genital clasping – total time that
successful males remained clasped to the females by their genitals after the connubium.

All procedures used to assess the relationship between antennation and sexual
performance aimed at keeping interference with the specimens at minimum, and there-
fore reducing the stress caused by handling, as those populations are established in
reserves and their conservation status is unknown. In addition, we did not expose the
specimens to highly invasive procedures, such as the removal of antennas or their parts.

**Data analysis**

We assessed data normality with the Lilliefors test. We used the Pearson correlation
coefficient to test for a relationship between antennation and courtship duration, as well
as between frequency of successful copulations and courtship duration. The significance
of the correlation coefficient was measured with a *t* test.

To test for a relationship between the sexual performance of monitored males and
antennation, and between the sexual performance of monitored males and courtship
duration, we used a multiple linear regression. We used the same test to assess the
relationship between genital clasping in successful males and antennation, courtship
duration and sexual performance. The choice of this statistical model was based on the
use of the coefficient of determination ($R^2$) in curve-fitting tests, so the highest values
found indicate the best fits of curves in relation to the scores. We tested for differences
in sexual performance between successful and unsuccessful copulations with a Mann–
Whitney test (Zar 2010). The statistical analysis was run in the software BioEstat® 5.0
(Ayres et al. 2007) at a significance level of $\alpha = 0.01$.

**Results**

We recorded 200 copulation attempts, but 14 of these were considered incomplete and
excluded from the analysis, as they contained insufficient information. Hence, in 186
complete copulation attempts, we recorded 6344 touches with antennae.

We observed a single type of antenna movement. In all cases, males moved their
antennae alternately or simultaneously vertically (up and down), while they hit the head
or antennae of the female. This behaviour was recorded in pre-copulation and copula-
tion phases, but all successful males interrupted antennation while they were clasped in
the female genitals.

The number of copulation attempts carried out by the same male varied from 1 to 9
(1.65 ± 1.20) with a courtship duration of 41.15 ± 29.29 s and sexual performance of
1.08 ± 0.57 touches/s, regardless of copulation outcome.

Successful males showed more antennal touches (39.38 ± 27.41 touches) per court-
ship duration (32.30 ± 25.55 s; Figure 1(a)) than unsuccessful males (36.06 ± 23.66
touches; 50.66 ± 30.22 s; Figure 1(b)). The number of antennal touches and courtship
duration were significantly correlated in successful ($r = 0.867; t = 15.983; df = n−2;
$p < 0.0001$) and unsuccessful ($r = 0.882; t = 16.567; df = n−2; p < 0.0001$) males.
The sexual performance of males that had successful copulations varied from 0.57 to 3.90 touches/s (1.39 ± 0.61), and, among those, 76.7% (n = 66) showed values equal to or above 1.00 touches/s. The sexual performance of males that had unsuccessful copulations varied from 0.74 ± 0.25 touches/s, of which 88.7% (n = 71) showed values below 1.00 touches/s. Although the Lilliefors normality pointed out that our data were not normally distributed, sexual performance differed significantly (U = 672,000; Z(U) = 8.949; p < 0.0001) between successful and unsuccessful males.

The correlation between the copulation frequency in successful males and the courtship duration was negative and significant (r = −0.886; t = −16.919; df = n−2; p < 0.0001) – that is, the relative frequency of successful copulation decreased, while the courtship duration tended to increase.
The multiple regression analysis showed a significant F value ($p < 0.0001$) for successful males in copulations. Therefore, we rejected the null hypothesis and accepted the alternative hypothesis, as at least one of the independent variables, antennation or courtship duration, was related to successful copulations. Hence, unlike courtship duration ($F^{(2,163)} = 111.729; \ R^2_{\text{adjusted}} = 0.573; \ t_{(b1, X1)} = -14.813; \ p = 0.1096$), only antennation was significant ($F^{(2,163)} = 111.729; \ R^2_{\text{adjusted}} = 0.573; \ t_{(b2, X2)} = 13.107; \ p < 0.0001$) among partial regression coefficients. Antennation is the variable that best explains male success in copulations. In other words, males with better sexual performance, successful in copulation, tend to increase antennation and reduce courtship duration.

Among successful males, the time of genital clasping varied from 13 to 41 s ($27.26 \pm 6.30$ s). In addition, the multiple linear regression did not detect significant differences in genital clasping ($p = 0.154$). This variable showed no relationship with courtship duration ($F^{(3, 82)} = 1.786; \ R^2_{\text{adjusted}} = 0.027; \ t_{(b1, X1)} = 0.216; \ p = 0.829$), antennation ($F^{(3, 82)} = 1.786; \ R^2_{\text{adjusted}} = 0.027; \ t_{(b2, X2)} = 0.607; \ p = 0.545$) or sexual performance ($F^{(3, 82)} = 1.786; \ R^2_{\text{adjusted}} = 0.027; \ t_{(b3, X3)} = -0.054; \ p = 0.956$), even when we considered only successful males with a genital clasping time of at least 25 s and its relationship with the same variables ($F^{(3, 57)} = 3.580; \ R^2_{\text{adjusted}} = 0.114; \ p = 0.018$).

**Discussion**

In general, antennation may play different roles in the sexual behaviour of male wasps for orientation near the female (Rezende et al. 1995; Romani et al. 2005) or in courtship itself: a display structure in courtship (Boush and Baerwald 1967), a signal of excitement level (Vinson 1972), a structure for tactile stimuli (Vinson 1972; Beani and Turillazzi 1988; Battaglia et al. 2002; Romani et al. 2005, 2008), and a chemical stimulus to female receptivity (Isidoro et al. 1996; Bin et al. 1999; Guerrieri et al. 2001; Battaglia et al. 2002; Romani et al. 2003, 2005; Klopfstein et al. 2010; Steiner et al. 2010).

Our study on *S. ingens* is among the few experimental models that tested and classified relevant variables involved in the courtship of this species. In most cases, there were dichotomies or generalisations, mainly concerning the meaning of antennation and antennation time (the latter here denominated ‘courtship duration’), which resulted in several ways to measure and interpret the variables involved in courtship. These considerations expose some of the difficulties faced in comparing behavioural repertoires between hymenopteran species, due to the lack of sampling protocols that standardise concepts or procedures.

In male *Sphex ingens*, the antennation comprised a rhythmic behaviour of antennae (alternate or simultaneous movements) that started after the mount and persisted during the pre-copulation and copulation phases through touches on the head or antennae of females. Hence, in part we corroborated the descriptions by Souza et al. (2015), though we did not observe any other behaviour attributed to courtship preceding mount (i.e. stimuli such as movements of legs and mouth parts and wing fanning). Certainly, this pattern represents only one peculiar component of the courtship of *S. ingens* compared to other species. Hence, antennation in *S. ingens* is composed of simple antennal touches in pre-copulation and copulation phases.

Antennation is a form of communication frequently reported during mating in spheciform wasps, and it is usually described as brief and rhythmic touches between
mates *in copulo*, without more intense contact (i.e. coiling or stroking) [*Ammophila campestris* Latreille: Barends (1941) apud. West–Eberhard (1969); *Editha magnifica* Perty: Martins 1993; *SpheX pensylvanicus* Linnaeus: Kurczewski (1998); *Rubrica nasuta* Christ: Pimenta and Martins (1999); *Trypoxylon* (*Trypargilum*) *agamemnom* Richard: Buschini and Donatti (2012)]. This fact suggests that this type of antennation is shared among several Crabronidae and Sphecidae wasp species, but leaves doubts about its influence on copulation success (*stricto*) due to the lack of further details.

More intense contact with the antennas during courtship was recorded in other Aculeata species in pre-copulation or copulation phases [*Asitus phragmitis* Ferrière, *Leptomastix dactylopia* Howard and *Rhopus meridionalis* Ferrière: Guerrieri et al. (2001); *Aphidius ervi* Haliday: Battaglia et al. (2002); *Polistes dominula* Christ and *Vespa cabro* Linnaeus: Romani et al. (2005); *Trichopria drosophilae* Perkins: Romani et al. (2008); and some Diplazonidae species: Steiner et al. (2010) and Klopfstein et al. (2010)].

In general, successful male *S. ingens* antennated more frequently and had shorter courtship duration than unsuccessful males. Certainly, all males gave their best to have the best result during copulation. In *S. ingens*, the difficulty and stress imposed by inter- and intra-sexual conflicts during mating (see Souza et al. 2015) together with the maintenance of multiple copulations require high energy investment and increase physical wearing. Hence, it is likely that the recovery time in the post-copulation phase influences individual performance, and, consequently, the subsequent copulation status in males.

Males that had unsuccessful copulation remained in mounting position on females, which corroborates the trends recorded by Souza et al. (2015). In theory, a male which after an unsuccessful copulation attempt manipulates the exposure time of the female to other males may not only increase the probability to fecundate the female, but also decrease the probability of other males fecundating it. However, although this hypothesis is persuasive as a reproductive strategy, our results do not corroborate it, as the chance of males being successful in copulation decreases as courtship duration increases.

Romani et al. (2005) observed a relationship between antennation and courtship duration in successful male *P. dominulus*. However, the authors did not record significant differences in the duration of the antennal display between successful and unsuccessful male *P. dominulus*.

Barends (1941) apud. West–Eberhard (1969) suggested that in *Ammophila campestris*, male antennation might stimulate the female to facilitate genital intromission or stop resisting the copulation attempts by males. Other experimental studies have reported similar patterns (Bin et al. 1999; Guerrieri et al. 2001; Battaglia et al. 2002; Romani et al. 2005, 2008). In contrast, Souza et al. (2015) suggested that the energy invested in communication (e.g. antennation) during the mating of *S. ingens* might represent only excitement signals.

Apparently, the differences in sexual performance found between successful and unsuccessful male *S. ingens* corroborate Barends (1941) apud. West–Eberhard (1969) and the results by Bin et al. (1999), Guerrieri et al. (2001), Battaglia et al. (2002), and Romani et al. (2005, 2008), or even suggest a trade-off. In the latter hypothesis, if it was proven that sexual performances with long courtship duration (energy investment) were rewarded with more genital clasping, males would thus maximise their fitness through
higher sperm transfer to fertilise a larger number of eggs. However, the lack of dependence of genital clasping on antennation, courtship duration or sexual performance is not consistent with that hypothesis.

Souza et al. (2015) recorded that female *S. ingens* adopt a release behaviour after genital clasping during the copulation phase. Hence, it is possible that the genital clasping obtained by successful males in copulation attempts is directly controlled by female *S. ingens*, which explains the results found.

The relevance of the information recorded on *S. ingens* in undeniable, as it fills some gaps about the sexual behaviour of the species, especially in terms of sexual selection. Even if high antennation values (antennal display) are related to successful copulations, it is not possible to assure that this variable influences exclusively the copulation status, but only that males successful in copulation antennated more in a shorter courtship duration than others, and, therefore, showed better sexual performance. However, sexual performance does not guarantee higher genital clasping during successful copulations.

We could have considered as an alternative hypothesis for the high frequency of antennation in *S. ingens* the combined use of acoustic signals during courtship. Acoustic signals produced by stridulatory organs are not only species-specific, but also related to several behaviours in hymenopterans (Grasso et al. 2000; Morales et al. 2008; Barbero et al. 2009a, 2009b), including during mating (Alcock and Buchmann 1985; Mercier et al. 2007). However, this remains one of the most poorly understood behaviours in Apocrita.

Another convenient topic to be analysed is the histology of the antennas of *S. ingens*, as the secreting glands in the antennomera have been reported to be fundamental components of the sexual behaviours of some spheciform wasps. For Bin et al. (1999), Romani et al. (2005, 2008), and Steiner et al. (2010), the copulation success in many hymenopteran species is related to the joint use of antennation and secretions released by male antennal glands during courtship.

Hence, this information substantially increases the understanding of the antennation value for *S. ingens*, and could also support phylogenetic reconstructions about the character status (antennation in courtship behaviour) in Aculeata.

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**Disclosure statement**

No potential conflict of interest was reported by the authors.
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