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Sexual behavior of the digger wasp *Sphex ingens* Smith (Hymenoptera, Sphecidae)

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ABSTRACT

A species' mating system depends on its spatial distribution and temporal availability of mating opportunities, as well as on the resources that create these opportunities. In addition, for many species, courtship is driven by specific behaviors that precede and follow copulation. Although *Sphex ingens* is a taxonomically well known species of digger wasp, its ecology and behavior remain poorly known. Hence, we analyzed patterns and trends of sexual behavior, in order to understand whether courtship can persist in a polygamous mating system. We monitored by video wasp populations in Ilha Grande, southeastern Brazil. Based on the observed behaviors, we calculated stochastic probabilities with a Markov chain to infer on behavioral trends. We recorded four behavioral phases based on 19,196 behavioral acts observed in 224 copulation attempts. There were no significant differences in common behavioral acts between males and females. The copulation patterns, conflicts, and trends observed in *S. ingens* clearly show the influence of sexual selection in its promiscuous mating system.

Introduction

In several animal species, mating systems are affected by food availability and distribution, breeding sites, and potential partners. The courtship and copulation phases are observed in most mating events. Currently, there is consensus on the conflicts of interest between sexes during mating, and sexual selection is an important mechanism in the choice of an ideal partner.

Among hymenopterans, the spheciform complex (Ampulicidae, Crabronidae, and Sphecidae *sensu* Melo, 1999) comprises wasps that are usually solitary and have a broad behavioral repertoire, especially in terms of reproductive and nesting behaviors (Evans and O'Neill, 1978; Amarante, 1999; Melo, 2000; Alcock and Kemp, 2005). Males increase their reproductive success through adaptive strategies or specialization (Evans, 1966; Alcock, 1975; Kroiss et al., 2010), whereas females increase their reproductive success through multiple mating (Melo, 2000) or by changing and sharing nests after the choice of a partner with better attributes or abilities.

The digger wasp *Sphex ingens* Smith 1856 is a large sphecid, which is usually black and whose gaster and legs vary from partially to completely red (Bohart and Menke, 1976). It has been recorded in the Brazilian states of Bahia, Espírito Santo, Rio de Janeiro, and São Paulo (Amarante, 2002).

The ecology and the behavior of *S. ingens* in Brazil were studied by Piliackas et al. (2007) and Buys (2009), respectively. Although these studies comprise short-term preliminary assessments and casual observations, they are still considered pioneering in Brazil, as few scientists have tried to understand the natural history of *S. ingens*.

The greatest challenges of a detailed study on the ecology and behavior of a wild population of *S. ingens* are the seasonality of its breeding and its restricted distribution. However, the poor information available on the ecology and behavior of *S. ingens*, in particular in terms of its sexual behavior deserves more attention, for instance, on the type of mating, phases and acts of mating repertoire, sexual behavior trends, influence of the courtship in the process of mate selection and selection criteria of females.

Preliminary observations indicate that the *S. ingens* mating system is polygamous, and the selection of partners does not occur through the courtship behavior. For this reason, we asked: how extensively does courtship behavior coexist in a polygamous mating system? Hence, the present study aimed at describing and analyzing the mating patterns and trends of the digger wasp *S. ingens*, aiming at advancing the knowledge of its nesting dynamics.

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Materials and methods

Study area and sampling design. Ilha Grande, a coastal island, is located in the municipality of Angra dos Reis, state of Rio de Janeiro, southeastern Brazil. It is a fragment of the coastal massif with a rugged relief, and has approximately 19,300 ha. Its predominant vegetation type is montane and submontane forest (Veloso et al., 1991). The Praia do Sul State Biological Reserve (RBEPS) covers 18.6% (3.600 ha: 23° 10′ S–44° 17′ W) of Ilha Grande's area, and harbors in nearly all its area a continuous complex of Atlantic Forest, which comprises forest environments (*sensu stricto*), *restinga* forests, mangroves, lagoons, shrubby *restingas*, rocky shores, and the beaches Meros, Aventureiro, Demo, Sul, and Leste (FEEMA, 2008).

We delimited transects above the high tide line and in foredune areas on Aventureiro Beach to find nesting sites. When we found a nesting site we delimited the area. In each nesting site, we captured males and females, marked their mesoscutum with colored non-toxic paint (Martins, 1993), and released them for individual identification and behavioral analysis.

We daily monitored *in copulo* pairs formed randomly with exchange of individuals, using a digital camcorder and a chronometer. The sampling effort totaled 131 h of observation, comprising the first fortnight of January 2010 and the first and second fortnights of January 2011. However, only 50 h were selected for analysis, i.e., 45 h of observation including all recorded copulations plus 5 h of observation used to interpret the mating behavior of the species.

At first, in order to interpret the behaviors we used the *ad libitum* method (Altmann, 1974), which is based on the behaviors that precede, trigger, and end copulation attempts, whereas for quantitative observations we used the sequence sampling method (Altmann, 1974). These procedures allowed the construction of a flow chart with the observed behaviors, in order to support the analysis and the construction of another flow chart on the conditional probabilities of occurrence and formation of stochastic processes (Gottman and Roy, 1990).

All procedures of the present study complied with the guidelines of the permit for scientific research #002/2011 issued by the Directorate of Biodiversity and Protected Areas (INEA-RJ). The captured specimens were deposited as vouchers in the Natural History Collection of the Federal University of Piauí (CHNUFPI: Hymenoptera Collection), *campus* Amilcar Ferreira Sobral: CHNUFPI(HYM)0002, CHNUFPI(HYM)0003, CHNUFPI(HYM)0004, and CHNUFPI(HYM)0005.

Statistical analysis

We transformed the absolute frequencies of the behavioral acts that compose the behavioral states into relative frequencies. We submitted the frequency of behavioral acts (state) common to males and females to a chi-squared test and logarithmized them to reduce the variation of frequencies whenever necessary. We modeled the relative frequencies of behavioral states with a Poisson distribution and a Markov chain, in order to estimate conditional probabilities and formation of stochastic processes. We ran the analysis using an add-in for Microsoft Excel® developed by the Operation Research Group of the University of Texas. We submitted the comparison between the Poisson distribution and the Markov chain to a Kolmogorov–Smirnov test ($p < 0.01$). All statistical analyses were made using free software.

Results

We analyzed 224 copulation attempts in 137 randomly formed pairs with interchange of males and females. The behavioral repertoire was divided in four phases: identification, pre-copulation, copulation, and post-copulation, based on a total of 19,196 behavioral acts distributed in 24 sexual behaviors (Table 1).

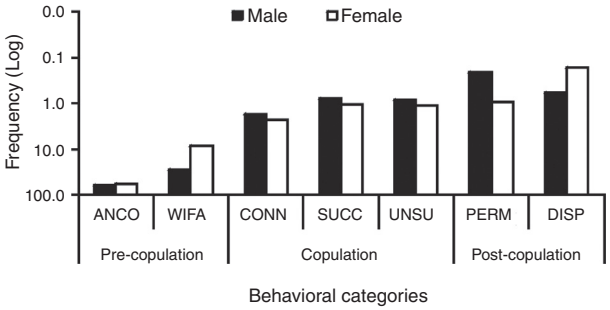

Fig. 1. Comparative fluctuation between the logarithmized and non-significant frequency ($x^2 = 16.622$, df $= n - 1$, $p < 0.01$) of the common behavioral acts of *Sphex ingens* Smith 1856 (Hymenoptera, Sphecidae). The common behavioral acts were: antennation (ANCO), wing fanning (WIFA), connubium/*strict* copulation (CONN), genital clasping/successful copulation (SUCC), no genital clasping/unsuccessful copulation (UNSU), permanence of males in the nesting arena (PERM), and dispersion/males leave the nesting arena (DISP).

Female mating behavior was composed of nine exclusive behaviors (2319 behavioral acts, 12.0%), whereas males showed eight exclusive behaviors (940 behavioral acts, 4.8%). Seven behaviors were common to both sexes (15,937 behavioral acts, 83.0%), but there was no difference between sexes ($x^2 = 16.622$, df $= n - 1$, $p < 0.01$) (Fig. 1). The most frequent mating phases in both sexes were pre-copulation and copulation, and behavioral acts related to communication were significant and recurrent in these phases.

Description of the sexual behavior based on the observed behavior

The identification phase consisted of visual recognition and male assault against females ($n = 155$), which were engaged in activities in their nests or were seized while flying over the nesting site. All approaches recorded were aggressive, preceding the attempt of immobilization, corroborating the existence of coercive copulation. The success in immobilization of females was 80.0% ($n = 124$) among all approach attempts (Fig. 2). In 18.7% of the cases the males could not immobilize the females or were rejected before any attempt, as the females were always aggressive.

The beginning of pre-copulation is characterized by males mounting females, followed by intensive communication, culminating in the extrusion of the aedeagus before its intromission in the female's genital opening. In some cases males rubbed the aedeagus laterally on the females' gaster before the intromission, whereas females hindered the copulation by curving their gaster.

In the copulation phase, receptive females positioned their gaster parallel to the substrate for aedeagus intromission. Contraction and bending movements directed the genital clasp to assure reproductive success. Females showed self-cleaning behavior during genital clasping (Fig. 3), and then were stimulated to adopt a disengagement behavior.

In post-copulation, males cleaned their genitals after they were disengaged. We observed both dispersal and permanence behavior in nesting arenas after disengagement in the post-copulation phase in males and females. Most females remained in the nesting arena (84.8%) and only a few dispersed (15.1%), whereas males showed the opposite behavior with higher dispersal (73.2%) than permanence (26.7%) in nesting arenas. We observed among males that remained in the nesting arena after effective copulation a decrease in motor activities reflected in low antenna mobility and wing fanning, characterizing a recovery period of 124.10 ± 39.30 s before a new copulation attempt.