Systematics, Morphology and Biogeography

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

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A B S T R A C T

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
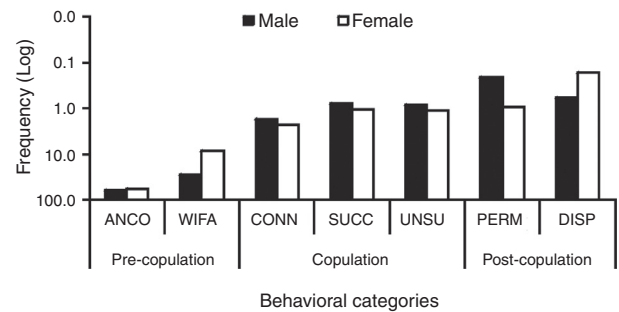

Fig. 1. Comparative fluctuation between the logarithmized and non-significant frequency ($x^2 = 16.622$, df $= n - 1$, $p < 0.01$) of the common behavioral acts of *Sphex ingens* Smith 1856 (Hymenoptera, Sphecidae). The common behavioral acts were: antennation (ANCO), wing fanning (WIFA), connubium/*strict* 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).

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).

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.

Table 1
Sexual behavior recorded for male and female digger wasps *Sphex ingens* (Smith 1856) (Hymenoptera, Sphecidae).

Behavioral acts	Abbreviation	Description
Recognition and assault	REAS	Males recognize visually females and move towards them.
Immobilization	IMOB	Males assault females directly for a copulation attempt. Males usually immobilize females using the first pair of appendages.
Aggressive display 1	DIS1	Behavioral act characterized by partially opened mandibles and vertical inclination of the body on the last appendages.
Confrontation	CONF	Behavioral act associated with DIS1, characterized by aggressiveness and advancement of females against males. It is usually triggered by lateral or frontal immobilization attempts.
Rejection	REJE	Behavioral act characterized by the refusal of the partner during lateral or frontal immobilization attempts. This act was also observed when a male underwent many unsuccessful copulation attempts.
Mount	MOUN	Recurrent behavioral act after a successful immobilization. Males remain on top of females to begin the pre-copulation sequence.
Extrusion	EXTR	Extrusion of the aedeagus for the intromission in the genitals of females.
Rubbing	RUBB	To laterally rub the aedeagus on the female's gaster before genital intromission.
Curvature of the gaster	CUGA	Females bend their gaster in general to prevent the access of males to the female's genital opening.
Antennation	ANCO	Antenna communication.
Wing fanning	WIFA	Wing fanning communication.
Aedeagus intromission	AEIN	Aedeagus intromission in the female's genital opening.
Aggressive display 2	DIS2	Behavioral act characterized by partially opened mandibles and intense antenna vibration.
Swaying body movements	SWAY	Unsociable behavioral act characterized by swaying body movements in the attempt to dislodge the male.
Drumming	DRUM	Consists in knocking several times the first pair of appendages against the substrate.
Connubium	CONN	Sexual activity marked by copulation dynamics composed of gaster contraction and bending movements.
Unsuccessful copulation	UNSU	No genital clasping occurs after connubium, characterizing an unsuccessful copulation attempt.
Permanence of mount	PEMO	Permanence of males in the mount position to begin a new copulation attempt.
Genital cleaning	GECL	Males clean their genitals using the third pair of appendages.
Genital clasping	SUCC	Genital clasping characterizing the copulation success of the male. Males clasped during copulation bend their bodies vertically on the last pair of appendages, and may twist their gaster laterally or maintain themselves in dorsal decubitus.
Genital disengagement	DISE	Behavioral acts of release after genital clasping. Females shove males using the third pair of ambulatorial appendages, drag them on the ground, or make flight attempts.
Self-cleaning	SECL	Usually performed by the female during the genital clasping, comprising the cleaning of antennae and first ambulatorial pair of appendages.
Permanence	PERM	Males remain in the nesting arena.
Dispersion	DISP	Males fly away from the nesting arena.

Sexual behavior: behavioral trends

The conditional probabilities of transition differed significantly between the Poisson distribution model and the Markov chain ($D_{max} = 0.240$, df $= n - 1$, $p < 0.01$: Kolmogorov–Smirnov), so that the vectors of limiting probabilities were built according to the Markov chain. The predictions derived from the Markov chain corroborated the observation that the behaviors exhibited during mating differed between males and females in terms of observed transition of behavior. However, sexual behaviors recorded *in loco* (observed behavior) in females, such as eye and antenna cleaning with their first pair of ambulatorial legs during genital clasp, dragging on the ground, and the attempt of flight with clasped males, were considered irrelevant and, hence, excluded from the analysis.

The results expressed by the diagram of the Markov chain highlighted that the behavioral transitions in communication including the antennation (7.9%) and wing fanning (21.4%) behaviors during pre-copulation and copulation have weak influence on the mating behavior of *S. ingens*.

The transition of the agonistic behaviors displayed by females during the identification (aggressive display 1: 10.3%, confrontation: 33.3%, and rejection: 33.0%), and copulation phases (aggressive display 2: 24.5%, swaying body movements: 31.1%, drumming: 64.3%, and rejection: 45.9%) indicate a strong trend to

Fig. 2. Sequence of the phase of identification and pre-copulation: (A) immobilization attempts by males while the female is supplying its nest with prey, (B) efficient immobilization of the female and mount in the nesting area, (C) aedeagus extrusion. Female shows a mixed behavior of receptiveness (last pairs of appendages up) and aggressiveness (partially opened mandibles).
Photo by: Jonas Pederassi.

Fig. 3. Sequence of the copulation phase: (A) beginning of aedeagus intromission. Copulation during nest digging – female carrying a clod of sand. (B) Connubium, gaster's contraction movements. (C) Connubium, gaster's bending movements. (D) Successful copulation – clasping of clasping organs. Male with the body vertically inclined and female self-cleaning.
Photo by: Jonas Pederassi.

select males. Another trend pointed out by the analysis was the attempt of males to remain mounted on females (47.9%) when copulation attempts were unsuccessful (Fig. 4).

Discussion

In the digger wasp *S. ingens*, even though males and females showed common behavioral acts during mating, differences in the frequency and diversity of these acts indicate different energy investment between sexes. Historically, the description of mating events in hymenopterans is characterized by different efforts and methods, which hinder comparisons.

However, although a behavioral similarity among species between copulation and mating phases has been described for some hymenopteran species, such as *Mormoniella vitripennis* Walker (Barrass, 1960, 1961), *Campoletis sonorensis* Cameron (Vinson, 1976) *Brachymeria intermedia* Nees (Leonard and Ringo, 1978), *Apanteles glomeratus* Linnaeus (Tagawa et al., 1985), *Ascogaster reticulatus* Watanabe (Kainoh, 1986), *Editha magnifica* Perty (Martins, 1993), *Nasonia vitripennis* Walker (Assem and Werren, 1994), and *Rubrica nasuta* Christ (Pimenta and Martins, 1999), the details of the behavior of *S. ingens*, as well as the variation in behavioral acts, their sequence, time, and frequency differ from those of other wasp species.

The confrontation and rejection behaviors recorded in *S. ingens* were common and present in all mating phases between males and females. According to Cordero and Eberhard (2003) pre-copulatory confrontations indicate the existence of conflicts between sexes and sexual selection, which favors manipulative males in coercive copulations. The resistance of females to the antagonistic behavior of males may select individuals according to their capacity of individual manipulation (signaling vigor and fitness) in clasping the female as it tries to get rid of the male (Allen and Simmons, 1996).

In *S. ingens* coercive copulation is an alternative strategy of males in response to the constant aggressiveness of females, as the latter use this criterion to select partners.

In *S. ingens* females, the larger number of copulation attempts in relation to the phase of nest construction (digging the tunnel or supply chamber) reflects a high energy investment, which makes them more evident in their respective arenas and nests, and justifies the trend of remaining in the nest after a copulation attempt, regardless of the result. Evans et al. (1976), Jang et al. (1996), and Melo (2000) consensually affirmed that most time and energy of females of the family Sphecidae is invested in maternal care in the form of construction and provision of nests during their reproductive life.

Male *S. ingens* were able to copulate repeatedly with females in the nesting site at any phase of nest building. This results in an intensive daily copulation activity that involves a relevant investment of time and in part corroborates the studies by Genaro (1998) on the species *Sphex jamaicensis* Drury. In several insect species the occurrence of multiple copulations suggests the existence of cryptic female choice (Ebehard, 1996), sperm competition (Parker, 1970), reduction in the female's spermatheca or that one or few copulations are not enough for the females to obtain enough sperm for a maximum production of offspring (Ridley, 1990), and even physiological deficiencies in the reproductive system of males (Martins et al., 2004).

Several studies reported that the courtship and copulation of many hymenopterans consist of movements of wings, legs, antennae, and mouthparts of males (Barrass, 1960, 1961; Mathews, 1975; Vinson, 1976; Leonard and Ringo, 1978; Tagawa et al., 1985; Kainoh, 1986; Martins, 1993; Assem and Werren, 1994; Pimenta and Martins, 1999). The sequence of these movements varies accordingly between species and is repeated by a receptive female (Mayr, 1973; Assem, 1986). Although these studies suggest the existence of visual stimuli that precede mount, we did not observe
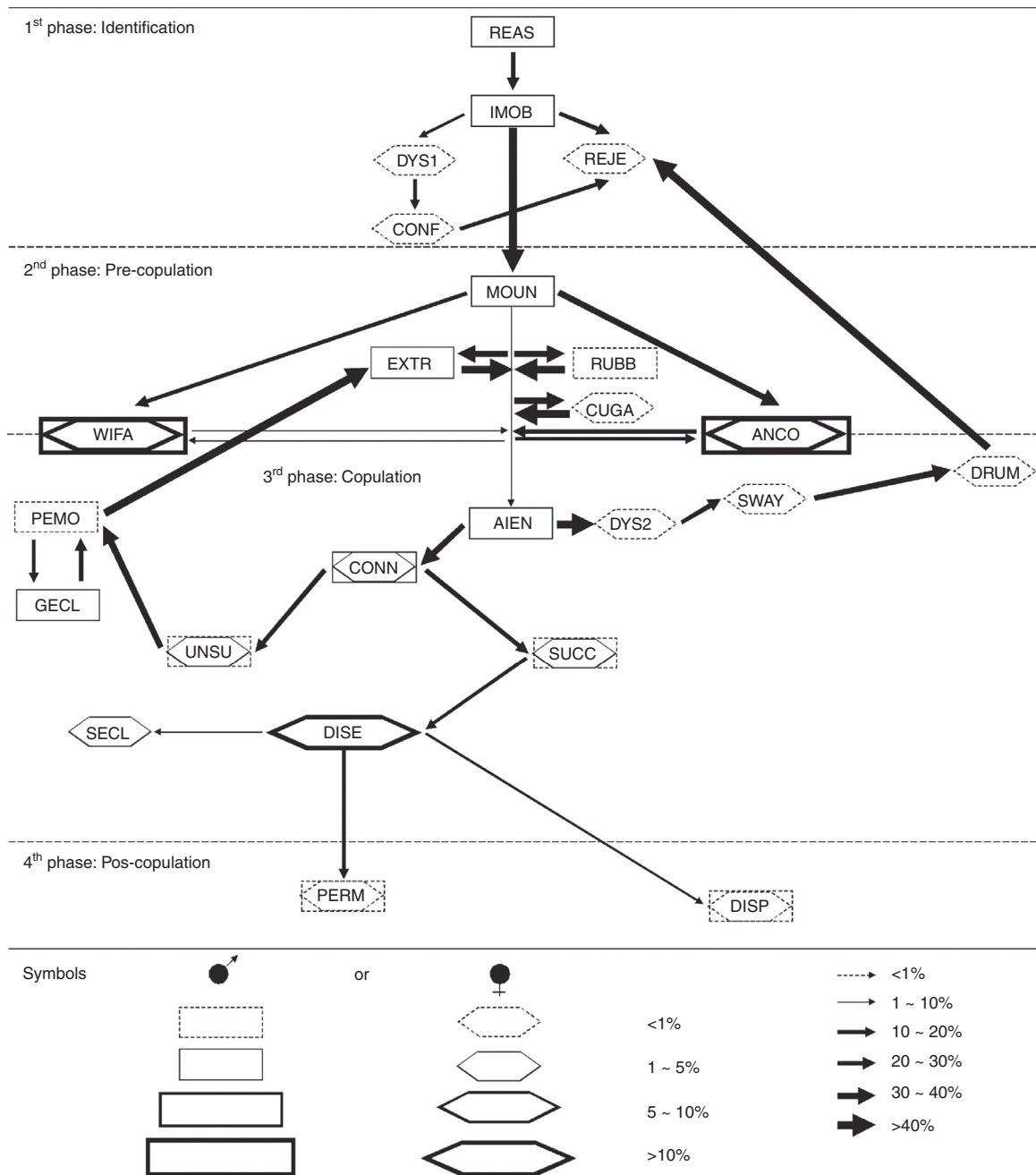
Fig. 4. Diagram representing the Markov chain for the sexual behavior repertoire of the wasp *Sphex ingens* Smith 1856 (Hymenoptera, Sphecidae). Symbols represent sexes. Symbol size and line thickness represent the frequency of occurrence of each behavior. Arrowheads represent the transition from one behavior to the next and arrow thickness represents the frequency class.

any pre-copulation gestural behavior in *S. ingens*. The lack of these behaviors in *S. ingens* results from the influence of the promiscuous mating system and from the way females select their partners.

Presumably, the energy spent in intersexual communication in *S. ingens* does not support that this behavior influences courtship, but would represent the exchange of stimuli used in conspecific recognition, as suggested by Mayr (1973), or general excitement signals. However, more specific tests on the performance of antennation and its influence on the successful and unsuccessful mating could clarify the function of this behavior. Furthermore, it is possible that in *S. ingens* pheromones are the only expressions of female receptivity, as we observed males trying to copulate with prey left by females at the entrance of nests. This behavior was also observed

in studies with other species carried out in the laboratory (Barrass, 1960, 1961; Mathews, 1975; Vinson, 1976).

Other aspects of sexual behavior of *S. ingens*, that would expand the understanding of its reproductive behavior, refer to the adjustments, disputes and strategies adopted by males to increase their reproductive success. Apparently, preliminary tests on the collected specimens suggest that there are size differences between the two sexes, as well between males with territorial and patrol behavior. Therefore, differences in size and behavior could influence individual fitness, with consequences to the results of mating disputes, and in the frequency of the reproductive success.

Our analysis corroborates that the mating system and female aggressiveness result in low sexual selectivity and a decrease in

courtship effort by males, and, hence, favor the maintenance of coercive copulation. They also suggest that the ability of males to manipulate the females during copulation is the main requirement for a successful copulation. Hence, the decrease in courtship effort by males is an alternative strategy to energy-demanding strategies based on elaborated courtship displays, considering the way that copulations occur, number of copulation attempts observed and constant confrontation with rival males in the present study. The escalation of female aggressiveness is an antagonistic sexual selection criterion different from classic forms found in the literature in terms of assessment of attributes or courtship rites. In addition, although coercive copulation is not an exclusive strategy among insects, it is rare in solitary wasps, in particular sphecids.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgments

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