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Territoriality and Mating Behavior of *Sphex pensylvanicus* L. (Hymenoptera: Sphecidae)

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Abstract.—Daily observations were made on nine individually marked males of *Sphex pensylvanicus* in upstate New York during 25 July–8 August 1982. Males occupied territories on or near a grate atop a storm sewer drain in which 12 females nested. They obtained honeydew at a maple tree and slept and fed on white sweet clover growing on a nearby hillside. The following maintenance and reproductive activities of males were defined: (1) perching at stations, (2) swivelling, (3) cleaning, (4) wing raising, (5) defecating, (6) spontaneous flights, (7) feeding flights, (8) pouncing on conspecific males, (9) pursuit flights, (10) grappling, (11) trailing conspecific females, (12) clasping conspecific females, and (13) copulation. Aggressive interactions between territorial conspecific males occupied more time than all other maintenance and reproductive activities combined.

Almost nothing was known about the behavior of male solitary wasps until Lin's (1963) study of male territoriality in *Sphecius speciosus* (Drury), the cicada killer. Recent interest in male behavior surfaced following the revival of Darwin's (1859) sexual selection theory, especially as championed by Trivers (1972) and his contemporaries. The activities of male solitary wasps are primarily aimed at obtaining matings. Males feed on nectar, rest on plants or in burrows, or bask in the sun when not in pursuit of females (Evans and O'Neill 1988). Males of most species of Sphecidae are free from parental duties and their reproductive success is solely determined by the number of eggs they fertilize. In other words, males of most species contribute little more than genes to their offspring.

Male solitary wasps tend to emerge before the females, a phenomenon known as protandry (Evans 1966). Circumstantial evidence suggests that females of most digger wasps mate only once during their lifetime (Alcock et al. 1978). Although nesting may extend for several weeks in certain species of Sphecidae (Hager and Kurczewski 1986, Kurczewski 1997), copulations in most species take place only during the first week or two. The majority of contacts between males and females do not end in successful copulation (O'Neill 1979). Once females are actively nesting, they rebuff all attempted matings by males (Evans and O'Neill 1988). The relative low fecundity of the females may mean that they actually gain little from additional matings (O'Neill 1985). Alcock et al. (1978) address the costs and benefits associated with multiple matings in species of aculeate Hymenoptera.

Territoriality, as defined by spacing, maintenance of stations, and aggressive encounters between conspecific males, does not occur in all sphecid wasps (Hager and Kurczewski 1985). But, it can be exaggerated in some species (Minkiewicz 1934, Lin 1963, Evans and O'Neill 1988). Males may establish stations or territories near prominent landmarks on the ground (*Astata*, Minkiewicz 1934; *Tachysphex*, Kur-

czewski 1966) or emergence holes (*Sphecius*, Lin 1963), or they may scent mark plants to attract females to a site (*Philanthus*, Evans and O'Neill 1988). The establishment and maintenance of stations or territories clearly facilitates mating between resident males and females in the vicinity (Alcock et al. 1978).

Studies on the behavior of male solitary wasps lag far behind those on female nesting behavior (Evans 1966, Alcock et al. 1978, Evans and O'Neill 1988). Male solitary wasps are often smaller, shorter lived, and do not maintain a nest making them more inconspicuous to the average observer (Kurczewski 1966, Hager and Kurczewski 1985). Among the species of Sphecinae (R. Bohart and Menke 1963, 1976), many of the studies on male behavior involve the genus *Ammophila* (Turner 1912, Baerends 1941, G. Bohart and Knowlton 1953, Olberg 1959, Powell 1964, Hager and Kurczewski 1985). Little is known about territoriality and male behavior in the genus *Sphex* including the nearctic *S. pensylvanicus* Linnaeus, the Great Black Wasp of John Bartram (Rau 1944). Rigley and Hays (1977) noted dominance, grappling, and attempted copulation in a few males of *S. pensylvanicus*. Gillaspy (1962) described mating behavior in the nearctic *S. tepanecus* Saussure. Janvier (1928) noted perching and grappling in the neotropical *S. latreillei* Lepeletier. Surprisingly, nothing is known of male behavior in a common nearctic species, *S. ichneumoneus* (Linnaeus)(Brockmann 1980).

My paper presents new and interesting information on the behavior of males of *S. pensylvanicus* and provides a verbal outline of the mating system employed by this species. The literature on reproductive behavior in sphecids is depauperate and observations such as those reported herein are needed to rectify this situation. Territoriality and mating behavior in this species were observed concurrent with an investigation on the sequential daily activities of the females (Kurczewski 1997). I chronologically sequenced and described individual male behaviors, especially those connected with spacing, aggression, and copulation, and attributed possible significance to them, thereby adding to the overall knowledge of male behavior in the family Sphecidae.

METHODS

Males of *S. pensylvanicus* were observed on a daily basis, weather permitting, from 25 July to 8 August 1982 from 0730 to 2100 hrs (EDT). The study area was examined before and after these dates and there was no sign of male activity. One must assume, therefore, that the males had not emerged before 25 July and either had died or left the area after 8 August. Nine males each were color-coded by placing a drop of Testor's model paint on their mesoscutum with a tiny paint brush from which had been removed most of the hairs. The activities of these males were observed and recorded at or near a storm sewer grate for a total of 62.5 hrs during 10 of the 15 days that they were in evidence. The individual life spans of the nine males was only 10–14 days, with three males living an entire two-weeks-long period. I similarly marked all 12 females from this aggregation thus yielding a secondary sex ratio of 3:2 in favor of females. One male and one female each were collected before individually marking them and placed as voucher specimens in the insect museum of the State University of New York College of Environmental Science and Forestry, Syracuse, New York.

Territoriality in this species facilitated simultaneous observation of all nine males; however, some time was allocated to observe certain focal males more extensively during fixed observation periods. Individual male behaviors were described and chronologically sequenced. Particular emphasis was placed on reproductive behavior as it occurred near a storm sewer drain in which the females nested. Less

emphasis was placed on male maintenance behaviors such as feeding, sleeping, and basking in the sun that took place away from this site.

EMERGENCE AND LOCATION OF STUDY

Both males and females emerged from soil near a broken tile at the bottom of the sewer drain situated in an asphalt driveway beside the Marcellus Senior High School, Marcellus, Onondaga County, New York. Three males emerged on 25 July 1982, two days before the first female appeared. The emergences of the other six males shortly thereafter (27–31 July 1982) were interspersed among those of early emerging females. Behavior that represented aspects of territoriality such as spacing, maintaining stations, and aggression between conspecific males was focused on a 70 × 70 cm grate atop the 70 cm-deep drain in which the females nested (Fig. 1, Kurczewski 1997). Males also visited a maple tree 13 m south of the sewer drain in order to obtain honeydew, and slept and fed at a stand of *Melilotus alba* (white sweet clover) 55 m away (Fig. 2, Kurczewski 1997). Both males and females fed on the flowers of other plant species nearby but not as frequently as at the florets of white sweet clover, probably because this species was more abundant in the vicinity (Kurczewski 1997).

The nine males left their sleeping roosts on white sweet clover daily on warm sunny days, occasionally fed on nectar or basked in the sun, and then made low circling or figure-8 flights over the sewer grate as early as 0828–0837 hrs (EDT) at an air temperature as low as 16°C. They stationed themselves on and/or near the grate from 0845 to 1643 hrs, and once as late as 1818 hrs, at air temperatures of 16.5–26°C. Males interrupted this territorial activity to feed on the flowers of *Melilotus alba* from 1125 to 1800 hrs at air temperatures of 23–26°C. They circled the drain in flight between 1819 and 2019 hrs, alit briefly on or entered through openings in the sewer grate, but then quickly exited and flew to sleeping roosts. Males did not maintain stations at or near the grate during this time. They did not make extensive and intricate flights for the purpose of orientation to the immediate environs as did the provisioning females (Kurczewski 1997).

MALE ACTIVITY

The following activities of male *S. pensylvanicus* were delineated: (1) perching at stations, (2) swivelling, (3) cleaning, (4) wing raising, (5) defecating, (6) spontaneous flights, (7) feeding flights, (8) pouncing on conspecific males, (9) pursuit flights, (10) grappling, (11) trailing conspecific females, (12) clasping conspecific females, and (13) copulation. Definition and significance of these activities are as follows:

(1) *Perching at stations.*—Males perched on or near the sewer grate with mid- and hindlegs outstretched yet raised and wings folded flat on the dorsum. They periodically moved their head or anterior body from side to side. While perching, males moved their antennae or held them still in an upward and outward attitude. The forelegs were either "fishhooked" medially or held backward beneath the body, raised above the substrate, and moved back and forth slowly or in short rapid bursts. Positioning by certain males close to the grate openings gave them a decided advantage over males stationed farther away with respect to access to entering or exiting females. These males subsequently obtained more claspings and copulations than males stationed farther from the sewer grate (see below).

Following emergence and through the first week of nesting, males maintained stations near the female nesting site. Males spent much time at a preferred site or station; however, most males maintained several stations in close proximity moving from one to another throughout the day.

On 27 July 1982, five males perched at stations on or near the sewer grate. Two of the males occupied opposite ends of the grate, being only 50–70 cm apart. The other three males were located near the grate at cardinal points of the compass, each less than 1 m from the two males. The males near the grate were not allowed to approach the males on the grate any closer than this without being chased away. On the following day, four additional, newly emerged males took up stations near the grate less than 1 m from the older males. Nine males now maintained one or more stations within a diameter of 2 m from the grate. The two males stationed on the grate and a third male nearest the grate perched at their stations for periods of 20–150 min ($\bar{x}$ = 37.9 min, n = 37 observations), except for chasing away conspecific males, females, and other insects, and making periodic flights with no discernible function. The six most peripherally situated males, on the other hand, perched for an average of only 3.8 (<1–7) min (n = 41) and then flew away for 1–71 ($\bar{x}$ = 32.4, n = 41) min before returning. In other words, the three males nearest the grate spent most of their time on or near it whereas the six males positioned peripheral to the grate occupied most of their time away from it.

The two males perching on the grate often approached to within 30 cm of one another without any apparent sign of interference between them. When one of the males flew away to feed, the other male encroached on his territory often temporarily appropriating some of the stations. Such replacement implies that males compete for stations, the defense of which clearly represents a form of territoriality. The spacing distance of about 1 m between most territorial conspecific males probably diminished the amount and intensity of aggressive interaction between them and thereby increased their chance for successful copulation but I have no concrete evidence to substantiate this.

(2) *Swivelling.*—Males often moved or turned their entire body to face in a slightly different direction. This movement was made so smoothly that the wasps appeared to be on a swivel. Swivelling was, therefore, a ramification of perching. Change in vantage ground by certain males may have ensured that they would not miss viewing females approaching or exiting the drain.

(3) *Cleaning.*—Males frequently cleaned their antennae, compound eyes, and mouthparts with the forelegs, and their wings and abdomen with the hindlegs. Wing and abdominal cleaning followed 63 flights during which a male pursued another male, female, or other insect. Only five times did a male land from such a flight without cleaning. Cleaning of the antennae, eyes, and mouthparts occurred seemingly spontaneously with or without the presence of another insect.

(4) *Wing raising.*—Males perching at stations often held the wings outward at an angle or raised and flicked the wings repeatedly. The former behavior was not observed to be associated with any specific incident. Sixty-one times wing flicking was associated with the appearance of a conspecific male, female, or other insect. After the intruder passed by, the perched male either lowered the wings onto the dorsum or cleaned the wings with the hindlegs and then lowered them. Raising and flicking the wings followed by wing cleaning invariably followed the pursuit in flight of another male and landing (see above). The two males stationed only 50–70 cm apart on the grate often wing flicked upon visible movement of the other. Raising and flicking the wings may have represented an intention movement to fly as this behavior was performed usually at the appearance of another male, female, or other insect.

(5) *Defecating.*—The two males stationed on the sewer grate for long periods of time periodically discharged a viscous liquid from the anus to a distance of 10–20 cm.

Often, this fluid was squirted in two or three directions by the wasp moving his abdomen to a slightly different angle.

(6) *Spontaneous flights.*—Every 1–8 ($\bar{x}$ = 2.1, n = 78) min, a male made a short brief flight of no discernible function directly away from his station, turned 180°, and returned along the same route to resume perching. Such flights were often less than a meter in length and of only 1–2 sec duration, but occasionally they were as long as 3–6 m and several seconds in duration. They were usually made in different, sometimes opposite, directions from a station. Possible functions of these flights include moving into cooler strata of air to reduce body temperature or surveillance of the immediate area and its occupants.

Other flights made by males were slower, more deliberate, and longer in distance and duration. They were more or less straight in line, often repeatedly covered the same ground, were 1–2 m in length or longer, and invariably lasted for more than a second or two. Some flights took the form of repetitive short distance figure 8's. The longer flights possibly function in helping locate receptive females.

(7) *Feeding flights.*—Periodically, males temporarily left their perches and flew to a nearby maple tree where they obtained honeydew or to a stand of white sweet clover from which they gathered nectar. As many as six males were simultaneously seen in the maple tree or feeding on *Melilotus alba* from late morning to early evening. Flowers of other plant species nearby such as Queen Anne's lace or wild carrot, goldenrod, yarrow, and white clover were visited less frequently for nectar.

(8) *Pouncing on conspecific males.*—When males at adjacent stations moved closer than 30 cm apart, one of them often made a short pouncing flight at the other wasp. The latter frequently flew out of reach of the former and then sometimes was pursued in a low, sinuous flight for a short distance. Less commonly the two individuals, after making contact, grappled with one another. This behavior may have reinforced the spacing of individual males.

(9) *Pursuit flights.*—Males maintaining stations near the female nesting site frequently flew at other males flying close to the sewer grate or at neighboring males if they approached too closely. Two wasps stationed on the grate periodically chased more peripherally located males in sinuous or figure-8 flights, 1–2 m above the ground, to distances of 3–5 m. Some of these flights transformed into ascending spiral flights, 3–4 m high. Continuous pursuit flights sometimes lasted for as long as 1.5 min. Regardless of the form of the flight, as many as four or five males participated in a single chase with distances of 20–30 cm separating individuals in tandem. After several seconds, such flights broke up into pairs of males or three individuals involved in chases. Flights terminated when the participants returned to their respective stations on or near the grate. Some chases involving two or three males continued into and out of the sewer drain. Physical contact occurred only rarely between males in pursuit of one another. In such cases one wasp grasped another, both fell to the ground, they grappled for several seconds, separated, and then flew to respective stations.

In addition to chasing conspecific males and females, territorial males also pursued dragonflies, moths, butterflies, horseflies, and other wasps and bees. The initiation of chasing depended entirely upon the visible presence of another insect, especially a conspecific. When other males were in the vicinity, males left their stations, took flight, and were air-borne continuously until the visitors(s) left the area. The sight of a non-provisioning female entering or exiting through the sewer grate often incited males stationed nearby to act aggressively toward one another and this frequently led to pursuit flights. By chasing other males out of the immediate area, males stationed on or near the grate would have more mating opportunities

available to them. Such males, in fact, did obtain more copulations with females than males situated on the periphery of the aggregation. Where all males were viewed simultaneously, the three males perching on or near the grate obtained eight (67%) of the 12 observed matings while the six males positioned farther away gained only four (33%). The three wasps stationed on or near the grate drove away all other males and permitted females to freely fly into the nesting area. However, copulations were successful only with females exiting through openings in the grate. Copulations with females entering the sewer drain were invariably unsuccessful.

(10) *Grappling.*—When two males approached to within 30 cm of one another they leapt at each other, held one another in a venter to venter position with the legs, and bit with the mandibles. Such grappling occurred in both anterior-anterior and anterior-posterior body positions. Grappling invariably ensued when a resident male pounced upon an intruding male flying low near the grate. Such wasps either separated in flight and returned to their respective stations or fell to the ground, making a buzzing noise, and continued grappling. Males stationed next to one another on or near the grate grappled for 2–20 ($\bar{x}$ = 11.8, n = 13) sec, separated, and flew to respective stations. One male stationed on the grate twice grappled with and drove away a larger intruder from a peripheral station. On three occasions two or three grappling males fell through openings in the sewer grate, disappeared from view, and resurfaced in tandem flight 3–5 sec later. After exiting, the three grappling males resumed grasping one another in flight above the grate with the legs and continued biting with the mandibles. Bouts of grappling even took place within ascending spiral flights up to 3–4 m in height. Much grappling occurred when non-provisioning females flew into the area by-passing the stations of adjacent males. One to several males pursued such an incoming female, immediately bringing them into close contact with one another. They briefly grappled with each other, one chased another away, and the victor continued to pursue the female in flight. Spacing, an expression of territoriality in males maintaining stations near female nests, was clearly established through bouts of grappling. Such premier positions often facilitated successful copulation (see above).

(11) *Trailing conspecific females.*—During the height of male activity the trailing and/or pursuit of conspecific females was secondary to chasing other males. In fact, many females were allowed into the nesting area and permitted to land without being chased or contacted by males. Nonetheless, some non-provisioning females flying near but not entering the sewer grate were pursued by territorial males for distances of 1–4 m after which the male returned to his station. In addition, males stationed on the grate sometimes followed females in flight into and out of the sewer drain and often interfered with females making orientation flights. Orienting females were pounced upon, bumped, and jostled in mid-air before they flew away. However, males did not pursue females whose orientation flights took them away from the drain. Attempts by males to contact females in flight probably served as a prelude to mating, but other males in the vicinity constantly disrupted copulation efforts.

(12) *Clasping conspecific females.*—Males clasped females by flying onto their dorsum and holding them with the legs. Females so grasped were deprived of the use of their wings and either plummeted downward to the ground from heights of 30 cm to 2 m or glided onto a nearby lawn, 2–4 m from the grate. Such clasped wasps rolled over several times while making a buzzing sound as the female attempted to escape. Sometimes the male was dorsum down, still retaining his

grasp of the female which was also dorsum down with her legs dangling in the air. One pair remained clasped together for 3 min as they continually rolled over and twisted on the ground while making a constant buzzing sound. They eventually separated but the male clasped the female again and repeated his attempted copulation for an additional 1.5 min. Unsuccessful copulation in the form of clasping, however, usually lasted only 5–45 ($\bar{x}$ = 18.7, N = 14) sec. Following attempted copulation, males cleaned the sides of their abdomen alternately with the hindlegs and their eyes, antennae, and mouthparts alternately with the forelegs. Clasping of females by males preceded mating but most such engagements never went to completion.

(13) *Copulation.*—Twelve of 29 (41%) pairings that began as clasping culminated in several minutes-long matings. Genitalic union was not achieved in 17 pairings that dissolved after 5 sec-4 min ($\bar{x}$ = 47.8 sec) of clasping. The twelve apparently successful matings were observed between 1021 and 1231 hrs during 27–31 July 1982. This period, when males were 2–6 and females only 1–4 days old, represented the pinnacle of reproductive activity insofar as frequency of claspings and copulations. Attempted copulations were sparse before and after this time. Matings were not seen during the second week of a male's life.

Successful copulation proceeded through a sequence of behaviors. Males always mounted females dorsal side up in a head above head position. Usually, the male remained on top with the female on the bottom. However, sometimes the male was on his side or, rarely, on his back holding the female ventral side up with her legs dangling in the air. Regardless of orientation, the male retained his grasp of the female by using his legs to grip her wings, body, and legs.

In the beginning stages of copulation, a male stroked a female's antennae with his antennae. This behavior seemingly aided in keeping her acquiesced. When the female became restless, she sporadically produced a buzzing sound. In order to contact her genitalia, the male rubbed the sides of his abdomen against the underside of the female's abdomen. The male's abdomen had to be telescoped and the female's abdomen mildly contracted to execute coupling. The last half of his abdomen had to be twisted nearly 45° and the female's abdomen turned somewhat. Once coupling was achieved, periodic sound production ceased. There was some rhythmic abdominal movement from both participants during copulation.

Males and females remained coupled for an average of 5.1 (R = 2.5–14.0, N = 12) min. Following an apparently successful copulation, the female feebly attempted to release herself from the male by slowly moving her legs and antennae and twisting her head in an arc. In some cases, the female tried to break loose by walking on the substrate dragging the attached male behind. Coupling, separation, and recoupling of male and female occurred up to three times in certain pairs. The arrival of other males or, rarely, females often led to disruption of mating and, almost invariably, to dissolution of the pairing. Twice, intruding females entering the mix led to genitalic separation and cessation of mating. Seven times an intruding male mounted the first male while he was mating, dislodged him, and disjoined the coupling. Recoupling by the original pair was sometimes achieved after such a disruption.

Once, as many as three males attempted to copulate with a single female, the participants being stacked in a pile atop one another. The pile of bodies kept falling to one side, but the pedestal male retained his grasp of the female and the other males their grasp to one another. Whether the pile remained upright or fell onto its side made no difference in the respective positioning of the males, probably because

the pedestal male was holding the bases of the female's wings with his forelegs and ad infinitum. After 35 sec, the uppermost male flew away for a few seconds only to return and rejoin the pile. In his absence, the remaining two males each tried to make genitalic contact with the female by fencing for prime position with the ends of their abdomens. Sound production occurred on and off during the entire attempted copulation. After 4 min of remaining together, the participants separated and flew away without successfully mating.

Male activity summary.—The activities of four focal males stationed on or near the grate were observed and recorded for 30 min-long periods at air temperatures of 23–24°C between 1015 and 1553 hrs on 29–31 July 1982 for the purpose of summarizing and ranking them. Of the combined 120 min spent by these males, 67 (56%) min were utilized for flying, chasing, and grappling, 43 (36%) min for perching, swivelling, cleaning, wing raising, and defecating, 6 (5%) min for clasping and copulating, and 4 (3%) min for feeding on honeydew and the flowers of white sweet clover. The large proportion of time spent air-borne by these males coincided with the presence of conspecific males and females in the area. Ninety percent of the time (60/67 min) used for flying, chasing, and grappling by males stationed on or near the sewer grate included the intrusion of conspecific males stationed nearby.

DISCUSSION

Male solitary wasps often emerge one or a few days before the females (Evans 1966). This trend, known as protandry, and an overall shorter flight season synchronize male activity with female emergence (Evans and O'Neill 1988). Early emergence of males gives them an opportunity to mate with unmated, recently emerged females (Bulmer 1983). One-third of the males of *Sphex pensylvanicus* that I studied emerged two days before the remainder of the males and the first females. The early emerging males were more successful in establishing stations near the female nesting site than later emergents and this eventually resulted in a higher proportion of matings for these individuals.

Rigley and Hays (1977) noted a "dominance order" among males of *Sphex pensylvanicus* for about a week during the "latter part" of July before the females started provisioning. One male positioned himself nearer the female burrows than two other males, continually chased them from the area, occasionally caught and grappled with them, and temporarily drove them away. The "dominant" male "solicited" females at their burrow entrances by repeatedly flicking his wings, flew after females as they exited their entrances, clasped them in flight, disappeared from view, and then returned 2–5 min later to resume perching near the nests.

Behavior of male sphecid wasps is predominantly directed toward obtaining matings (Hager and Kurczewski 1985, Evans and O'Neill 1988). Males of many digger wasp species maintain territories or perches near female nests in order to gain a reproductive advantage (Lin 1963, O'Neill 1979, Evans and O'Neill 1988). Copulatory attempts near nesting sites underline the importance of territories or perches to facilitate mating (Alcock et al. 1978). In *Sphex pensylvanicus*, females often nest aggregatorily in one area (Reinhard 1929, Frisch 1938, Rigley and Hays 1977, pers. obs.). Males establish stations near the female nests, the two sexes are continually brought into contact with one another, and mating is expedited.

Male territoriality, as defined by spacing, maintenance of stations or perches, and aggression between conspecifics, has been demonstrated for a number of sphecids (Lin 1963, Evans 1966, Kurczewski 1966, Alcock et al. 1978, O'Neill 1979, Evans and O'Neill 1988, Hastings 1989). Applying this definition to *Sphex pensyl-*

vanicus, territoriality clearly is operational among the males (Rigley and Hays 1977, pers. obs.). In this species spacing and station maintenance and defense may function in reducing conflict between conspecific males and promoting successful copulation.

Although mating is the ultimate goal of male digger wasps, aggressive interactions between conspecifics are clearly the most conspicuous activities of territorial males (Evans and O'Neill 1988). More than 90% of the time spent by males of *Sphex pensylvanicus* during a three day-long observation period involved aggressive activities connected with territoriality. Males used most of this time in making flights, grappling with and pursuing other males, and vigorously defending stations against conspecifics. Males of *Sphex pensylvanicus* utilized only about 5% of their available time for clasping and mating. Some males, in fact, consistently ignored females flying into the area in order to pursue other males. However, if a male spends too much time on aggressive interactions with conspecific males, he wastes time and energy that could be used for locating and contacting females (O'Neill 1979).

Copulation in *Sphex pensylvanicus* is similar in configuration and relative positions of male and female to that of other sphecines, especially members of the genus *Ammophila* (Turner 1912, Baerends 1941, Olberg 1959, Powell 1964, Hager and Kurczewski 1985). In the former species, duration of coupling is apparently briefer than in species of *Ammophila* and the male and female abdomens are held outward rather than raised upward. Uncoupling and recoupling are characteristic features of copulation in both *Sphex* and *Ammophila* (Baerends 1941, Olberg 1959, Hager and Kurczewski 1985, pers. obs.). Coupling, separation, and recoupling in certain pairs of *Sphex pensylvanicus* occurred up to three times during one copulation event. Disruption of matings by conspecifics occurs frequently in *Ammophila* and *Sphex*. Two or more males attempting to mate with a single female and, in the process, disengaging the initial coupling appears to be a common strategy in both genera. In such a case an intruding male may benefit immediately or later via successful copulation with the disjoined female (Hager and Kurczewski 1985).

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