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Activity Patterns in a Nesting Aggregation of *Sphex pensylvanicus* L. (Hymenoptera: Sphecidae)

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Abstract.—Daily observations were made on 22 individually marked females of *Sphex pensylvanicus* L. in upstate New York in 1981 and 1982. Wasps nested in soil at the bottom of a storm sewer drain, obtained nectar from flowers, slept on the stems of forbs, and hunted and captured prey in trees on a nearby hillside. Their nourishment, nesting and predatory activities incorporated a distinct temporal series of flights to and from nests including (1) early to mid-morning returns from sleeping roosts; (2) periodic inspection returns; (3) exits to feed, hunt, and bask in sun; (4) prey transport; (5) returns to enlarge nests; (6) returns to nests at dusk; and, (7) exits to sleeping roosts. One-half of exits that followed morning or afternoon visits to nests, only one in three exits after placing prey in the nest, and fewer than one in five exits following nest enlargement or entry near dusk gradually transformed into orientation flights. Females spent more time inside their nests following pre-darkness returns than after morning returns from sleeping roosts, periodic inspection returns, or taking in prey.

Species of the sphecid genus *Sphex* comprise large, thread-waisted, ground-nesting wasps. Aside from *Sphecius speciosus* (Drury), the cicada killer, *Sphex pensylvanicus* Linnaeus is the largest sphecid in eastern North America. The females average nearly 30 mm in body length, are all black with black erect hairs on the head and thorax, and have violaceous tinted black wings (Bohart and Menke 1963). This species, the "Great Black Wasp" of John Bartram, is of historic significance as it was the first solitary digger wasp described from the United States (Rau 1944). *Sphex pensylvanicus* has a rather broad geographic distribution ranging transcontinentally across the United States into northern Mexico, except for the northwestern states (Bohart and Menke 1976). Some of the species of *Sphex* appear to be strictly solitary nesters. Females of other species such as *Sphex ichneumoneus* (Linnaeus), the Great Golden Digger Wasp (Ristich 1953), nest close together with two or more wasps rarely sharing the same nest (Brockmann and Dawkins 1979). Females of *Sphex pensylvanicus* also nest close together but it is uncertain whether they share a common nest.

Although the basic features of the nesting behavior of *Sphex pensylvanicus* have been studied in some detail, little is known about the daily periodic activities of the females. Reinhard (1929) and Frisch (1938), working together on this species, published separate articles under the name *Ammobia pennsylvanica* (L.). Their reports contained information on geographic distribution, seasonal occurrence, aggregation, nesting habitat, nest structure and dimensions, cell contents, prey selection, prey paralysis, prey transport, egg placement, and description and duration of egg, larva, cocoon, parasites, and hyperparasites. Rau (1944) described seasonal flight period, habitat, aggregation size, burrow construction, nest dimensions, cell contents, prey type, paralysis of prey, prey transport, nest entry, and egg placement of this species under the name *Chlorion* *pennsylvanicum* (L.). Krombein (1955) reported on the prey transport, prey paralysis, and provisions of one "*C. pennsylvanicum*" nesting among a dozen individuals in a bluff along a beach. Rigley and Hays (1977) noted flight period, aggregation size, reuse of old nests, burrow excavation including sound production and sonagram, prey type, and male activity of this species.

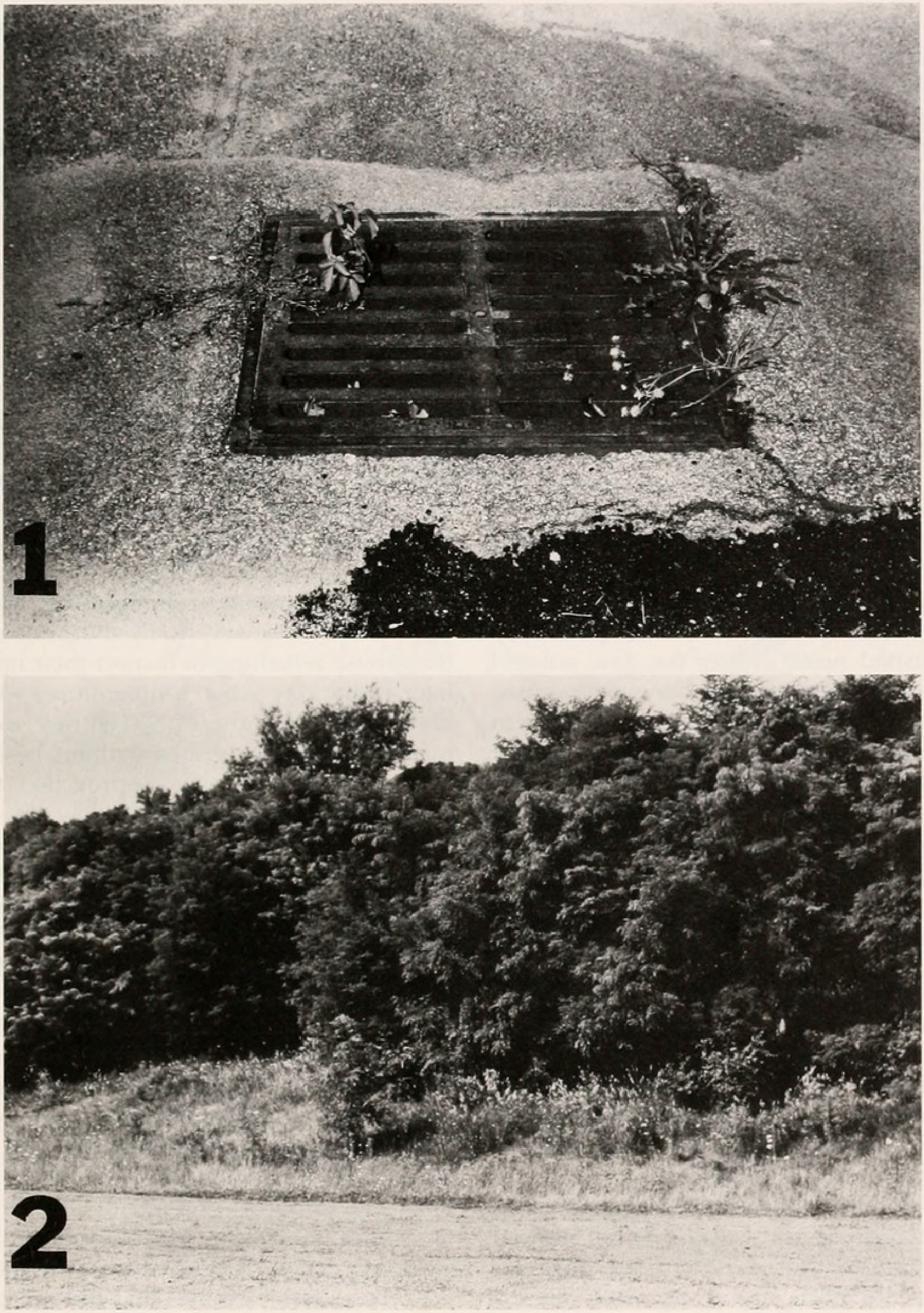
The objectives of my paper are to sequentially delineate some of the periodic daily activities of *Sphex pensylvanicus* in relation to time of day, air temperature, and season. Only sparse information of this kind exists for sphecid wasps and, therefore, such observations should be valuable to future researchers in this field. A recent study on *Sphex argentatus* Fabricius in India by Belavadi and Mohanraj (1996) comes closest to approximating the goals of the present paper. These authors delineated nest structure and dimensions, indicated time spent for various activities including provisioning and types of closures, and gave a flow diagram of nest building components. They presented a detailed time table for various daily activities but, unfortunately, did not define the activities listed in the table such as grooming, sitting alert, sitting, and chasing predators. Belavadi and Mohanraj (1996) found that excavating the main burrow, hunting for prey, and making the permanent closure utilized more than three-fourths of a female's observed activities. Brockmann and Dawkins (1979) prepared a time budget for *Sphex ichneumoneus* and found similarly that burrow excavation, searching for prey, and closing the nest utilized a considerable portion of a female's available time.

LOCATION OF NESTS

The aggregation of *Sphex pensylvanicus* I studied nested during 29 July–30 August 1981 and 27 July–1 September 1982 inside of a storm sewer drain situated in an asphalt driveway beside the Marcellus Senior High School, Marcellus, N.Y. (Fig. 1). The 70 × 70 cm iron drain cover had grates large enough to permit ready entry and exit by the provisioning and orienting wasps. In 1981 a total of 10 females nested inside this sewer drain. One of the wasps nested in the loosened mortar between the bricks of one wall of the drain. The nest entrance, 2 cm in diameter, was situated 41 cm below the driveway surface. The tumulus to this nest, consisting of pebble-sized pieces of mortar and measuring 10 cm long, 13 cm wide, and 5 cm high, was positioned 29 cm beneath the nest entrance at the bottom of the drain, or 70 cm below the driveway. The other nine wasps nested in a single aggregation in soil beneath a sewer tile located at the bottom of the drain. These females used the intact mouth of the tile, which was one-third filled with gravel and broken in several places, as a common vestibule. A torrential downpour on 2–3 September 1981 filled the bottom of the drain and submerged all of the nests except for the one in the brick wall. There was no sign of female activity at this site in 1981 following the rain. Nonetheless, 12 wasps emerged and nested beneath the same drain tile in 1982. On 12 August 1982, I discovered two additional nesting aggregations of this species inside sewer drains in the high school parking lot, 30 and 80 m NE of the first site. These wasps were not studied in detail because of the distance from the first aggregation.

METHODS

Individual wasps were observed daily, weather permitting, from 0730 to 2100, except for one day (19 August 1982) when I arrived at the nesting site as early as 0600 hrs (EDT). Their behaviors were arbitrarily separated into functional categories as defined under "Female Activity." Each wasp was color-coded to facilitate following her daily and seasonal activity. This was accomplished by marking the mesoscutum with Testor's model paint using a



Figs. 1–2. 1, Storm sewer drain in which females of *Sphex pensylvanicus* nested. Wasps entered and exited through openings in the drain cover. 2, Black locust stand and adjacent field of flowers where females of *Sphex pensylvanicus* hunted, fed on nectar, and slept.

tiny paint brush from which most of the hairs had been removed. Maximum longevity of females was 35 days for one wasp marked yellow. Only three of 22 wasps lived for longer than a month. 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.

FEMALE ACTIVITY

From early to mid-morning, *Sphex pensylvanicus* females left the upright vegetation on which they slept, flew to nests, entered, and exited with or without orienting or fed briefly or basked in the sun before arriving at the nest. Some females left sleeping roosts and returned to nests as early as daybreak. Individuals periodically visited nests during the day, entered, exited, and then fed on honeydew or nectar of nearby flowers, basked in the sun, or hunted, captured and transported prey. Nest enlargement frequently took place toward evening and preceded exits and flights to sleeping roosts. Females not enlarging burrows returned to nests at dusk, entered, exited, and flew to sleeping roosts (Fig. 3).

Female activity at or near nests arbitrarily was separated into the following components for analysis: (1) morning flights to nests from sleeping roosts, feeding stations, or basking places, entry, and exit; (2) orientation flights; (3) periodic flights to nests probably for the purpose of nest inspection and/or reorientation, entry, and exit; (4) nectar feeding; (5) prey transport flights, entry, and exit; (6) entry, nest enlargement, and exit; (7) pre-darkness flights to nests and entry; and, (8) exit flights to sleeping roosts. A companion paper examines the territoriality and mating behavior of this species (Kurczewski in prep.).

Returns from sleeping roosts.—Ninety-three observations of females returning from sleeping roosts, which comprised upright vegetation [predominantly *Melilotus alba* (white sweet clover)] on a hillside 55 m from the nesting site (Fig. 2), indicated that most returns were made between 0829 and 1038 hrs (EDT) on warm sunny mornings (Fig. 5). However, three females returned from sleeping roosts on 19 August 1982 as early as 0635, 0647 and 0655 hrs at an air temperature as low as 10°C. The earliest of these returns was made before sunrise. Successively later sunrises induced increasingly later morning returns to nests in females nesting over a period of several weeks. On rainy mornings, 17 flights (N=9 wasps) were made to nests within 48–69 min after cloud cover dissipated and the sun reappeared, regardless of time of day.

Females returning from sleeping roosts flew into the sewer drain more slowly than those returning to inspect their nests later in the day when temperatures were higher. Eighty-eight of 93 entries were made through the grates without hesitation. Five times wasps approached the drain cover, hovered near it, flew off, returned in flight 3–8 sec later, and entered. Once inside the drain, females inspected the opening into the drain tile by flying from left to right and vice versa while facing it. After entering the opening and disappearing from view, females stayed inside nests 7–59 min ($\bar{x}$=16.9, N=93) before reappearing inside the drain. They then spent 1–4 min ($\bar{x}$=1.5) flying in front of the opening, as described above, before exiting through the grates. Forty-eight of 93 exits gradually transformed into what I interpreted to be orientation flights. Forty-five times, the wasps abruptly flew away without making repetitive aerial maneuvers. Five of the females that did not orient made an orientation flight the previous evening. Other wasps that did not make orientation flights may have done so before I arrived at the nesting site.

Orientation flights.—Wasps made orientation flights during practically any time

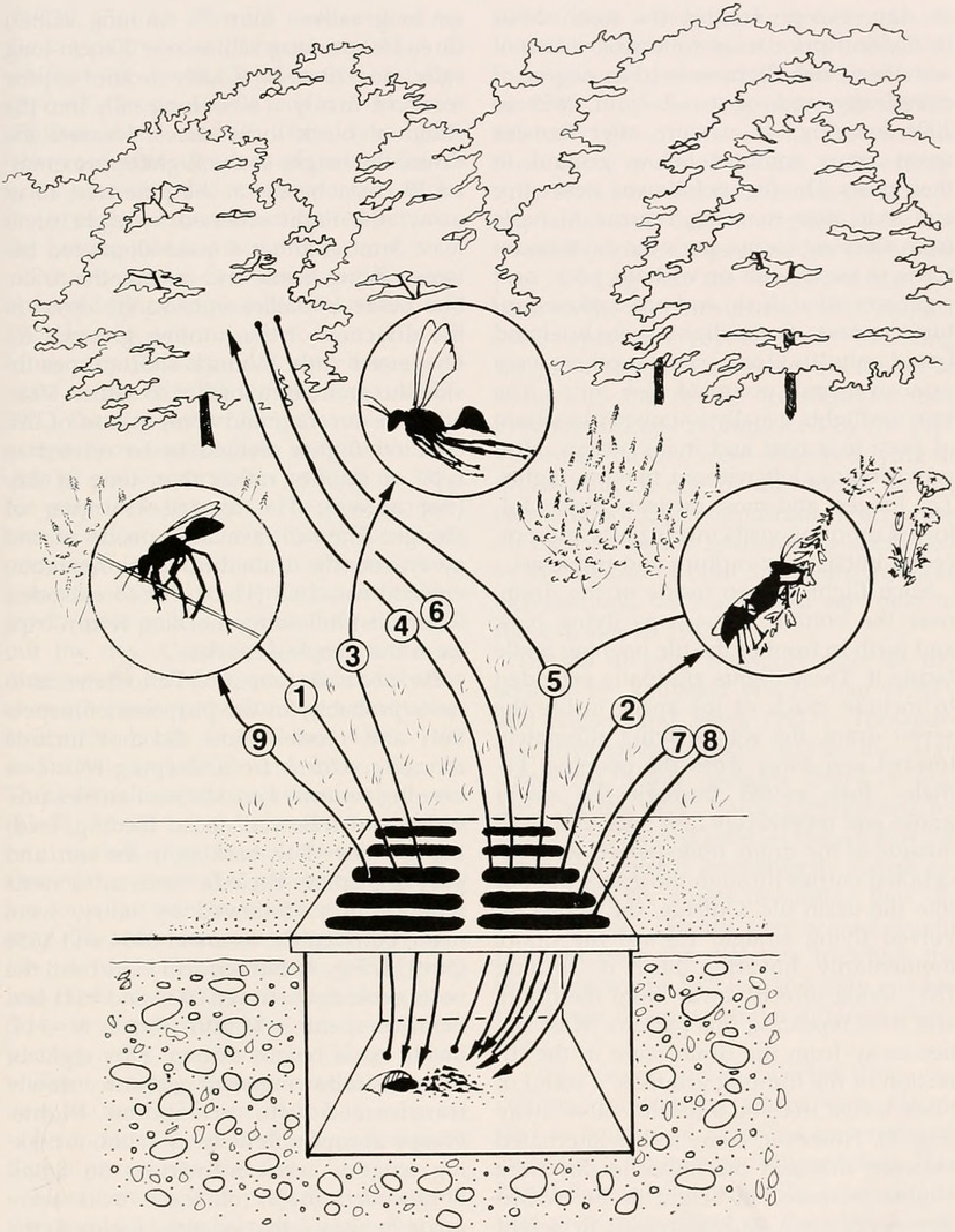


Fig. 3. Summary of daily flight activities of females of *Sphex pensylvanicus*. Numbered arrows designate flights as follows: (1) from sleeping roost; (2) to feed on nectar; (3) orientation; (4) to hunt in trees; (5) periodic return from flowers or trees; (6) prey transport; (7) return to enlarge burrow; (8) dusk inspection return; and, (9) to sleeping roost. Wasps in circles are sleeping and feeding on white sweet clover, respectively, and making an orientation flight (center).

of day, except around the noon hour (EST), and prior to or following different activities. Such flights varied in degree of complexity and occurred from 0859 to 2004 hrs (Fig. 4), usually after females spent many minutes below ground in their nests. The flights followed nest entry and exit after morning returns to nests from sleeping roosts, periodic daytime returns to nests with or without prey, nest enlargement at dusk, and pre-darkness returns to nests. Some flights were brief and lasted only 10–30 sec, whereas others were extensive and occupied 5–6 min. The briefest flights usually followed placement of prey in a nest and many wasps, after provisioning, left without making flights. The longest and most intricate flights followed morning visits inside nests and preceded initial prey capture and transport.

Such flights began inside of the drain, near the bottom, the wasps flying back and forth in front of the tile opening while facing it. These flights gradually extended to include much of the space inside the sewer drain, the wasps flying alternately toward and away from the opening. Females then exited through the sewer grates and repetitively flew back and forth outside of the drain, interspersed with occasional entries through the grates but not into the drain tile. Outside, the flights involved flying straight toward the drain, momentarily hovering near it, turning 180°, flying directly away from the drain, and then repeating this pattern. Most sallies away from the drain were in the direction of the hunting grounds, a stand of black locust trees on a hillside 60 m away (Fig. 2). However, some sallies alternated between this and the opposite direction. Flights increased in height as the wasps flew away from and decreased in height as they flew toward the drain.

The duration and complexity of such flights varied with different females. For example, one wasp began her air-borne maneuvers outside the drain by making two 15 cm-long sallies, then three 30 cm-long sallies, four 75 cm-long sallies, three 150 cm-long sallies, one 300 cm-long sally, one 13 m-long sally around a pine tree and, finally, a 60 m-long sally into the stand of black locust trees. Nearest the drain, the height of the flight approximated 15 cm, whereas at the pine tree, 13 m away, the flight attained a height of at least 3 m. Another female alternated between flying inside and outside the drain. She made 18 sallies outside the drain in the direction of the hunting grounds interspersed with 27 much shorter ones inside the drain, or a total of 45 sallies. Variation in duration and composition of orientation flights seemed to be related to type of activity rather than time of day (see above). The average number of straight line sallies made outside of and away from the drain during an orientation episode was 16.5 (11–31, N=45 episodes; 9 females) following morning return trips from the sleeping roosts.

Periodic visits to nests.—Periodic visits to nests probably for the purposes of inspection and reorientation did not include morning returns from sleeping roosts or evening returns. Periodic nest entries preceded and followed nectar feeding, feeding on honeydew, basking in the sun, and prey transport. Periodic returns to nests without prey, followed by entry, were made between the hours of 0934 and 1638 (N=114, Fig. 4). Subsequent exits from the nests occurred between 0939 and 1641 hrs. Females spent 1–30 min ($\bar{x}$=9.5, N=114) inside nests before exiting. Fifty-eight of 114 exits following such nest entry slowly transformed into orientation flights. Wasps abruptly flew away without making lengthy aerial maneuvers 56 times. Forty-seven (84%) of these exits were made by wasps that oriented earlier in the day.

Nectar feeding.—Females frequently visited flowers in nearby fields to obtain nectar. They were seen on flowers mostly during the late morning (1100–1200) and mid- to late afternoon (1400–1700) hours

(N=39, Fig. 5). Flowers most visited by the wasps in order of frequency were (1) white sweet clover, (2) goldenrod (*Solidago* spp.), (3) Queen Anne's lace or wild carrot (*Daucus carota*), and (4) white clover (*Trifolium repens*). Frequency of specific flower visits corresponded to the relative abundance of the plant species located between the nesting site and hunting ground.

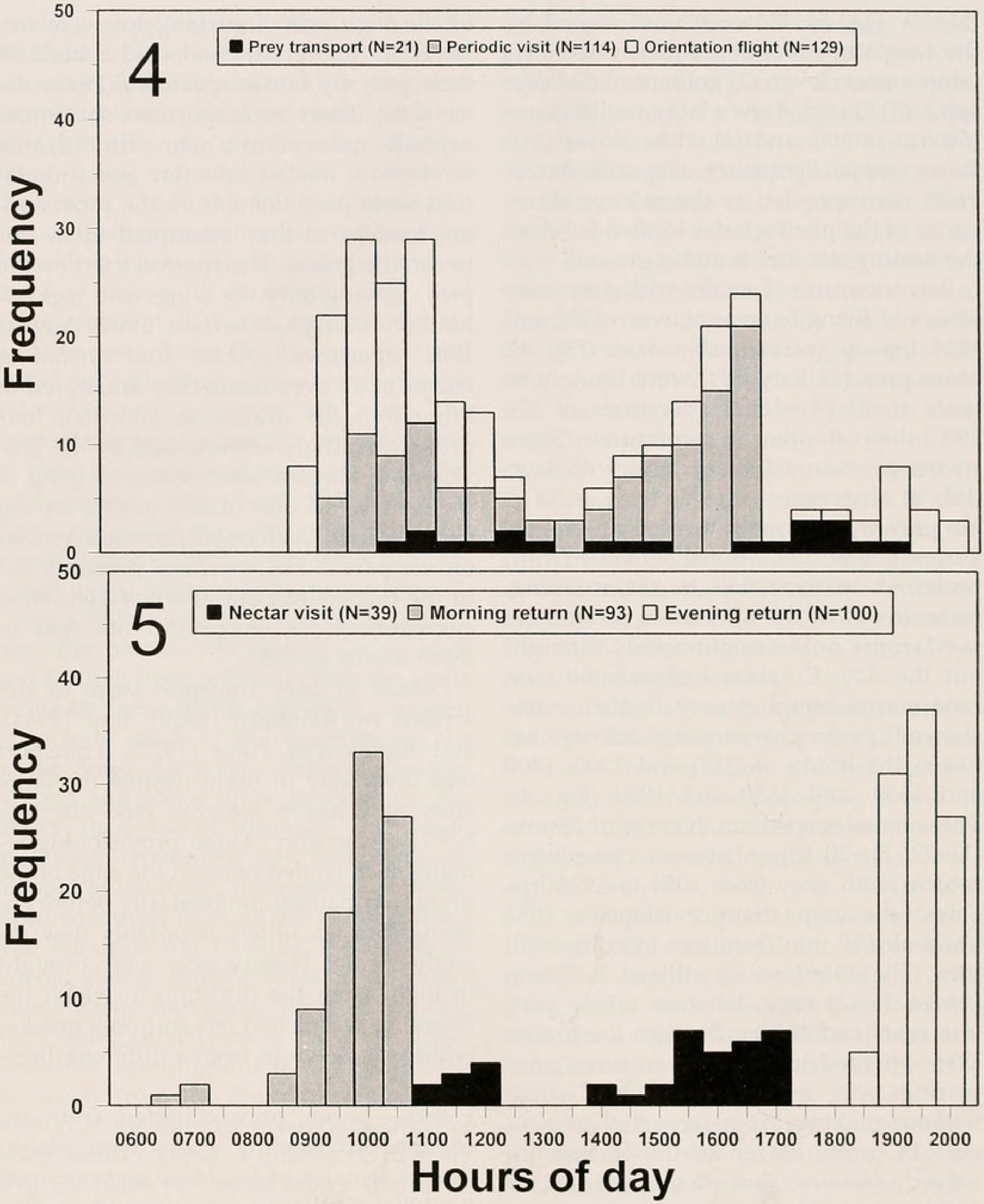
Prey transport.—Females with prey were observed flying to nests between 1032 and 1924 hrs on warm sunny days (Fig. 4). More prey (14 katydids) were brought to nests at air (shade) temperatures of 27–29°C than at other temperatures. Some wasps provisioned their nests with kaydids at air temperatures as high as 33°C. No prey were brought to nests at temperatures below 23°C. Some females (n=4) preferred to provision in the morning, some (n=6) in the afternoon, and others (n=2) more or less continuously throughout the day. Combined observations on nine wasps bringing prey to their nests showed peak provisioning activity between the hours of 1030 and 1300, 1400 and 1500, and 1630 and 1900 (Fig. 4). These females spent an average of 43 min (11–72, N=20 trips) between consecutive returns with prey from 1054 to 1924 hrs. One of the wasps that provisioned at 1032 hrs took 110 min from exit to entry with prey. The nine females utilized 2–17 min ($\bar{x}$=8.4, N=21 trips) between taking prey into nests and exiting through the grates. They oriented in flight seven times after placing prey inside nests. They exited without making extensive aerial maneuvers 14 times. Eleven of the 14 exits involved females that made orientation flights previously that day.

Most females with prey flew directly to their nests. In late July and early August, some provisioning wasps were pursued and jostled in flight by males attempting to mate. Nonetheless, these females retained their grasp of the prey and entered their nests. During mid-August, four wasps nesting inside the two sewer drains in the high school parking lot were followed in flight, harassed, and robbed of their prey by house sparrows (*Passer domesticus*). Three such sparrows sat on the asphalt pavement near the drains throughout much of the day and successfully stole prey items from the provisioning females as they attempted to fly between the grates. The sparrows fed on the prey, leaving only the wings and legs behind on the asphalt surface. On 18 August 1982, sparrows robbed four incoming wasps of 13 prey items they attempted to bring into the drains. In addition, four prey unwittingly relinquished by the provisioning females were observed lying at the bottom of one of the drains on the earthen floor. Such opportunistic activities on the part of the sparrows probably led to the demise of both *Sphex pensylvanicus* aggregations, as wasps did not nest in these drains in 1983.

Details of prey transport were as described by Reinhard (1929), Rau (1944), and Rigley and Hays (1977). Transport was invariably in flight despite the large sizes and heavy weights (566–716 mg, N=7) of the prey. Three provisioning females each landed once on the edge of the drain and paused momentarily before entering, but six others invariably flew directly inside. Twenty prey were brought in flight from the direction in which the orienting wasps had left and only one katydid was flown in from a different direction.

Prey.—Seven prey collected from incoming provisioning wasps were identified as females of *Scudderia septentrionalis* (Serville) (Orthoptera: Tettigoniidae). This katydid species is primarily arboreal and was seen ovipositing on the black locust trees mentioned above.

Prey paralysis included periodic movements of the antennae, mouthparts, and, rarely, legs, and rhythmic breathing movements of the abdomen. Similar descriptions of the paralysis of prey were



Figs. 4–5. 4, Time distribution diagram of prey transport flights, periodic visits to nests, and orientation flights of *Sphex pensylvanicus* females. 5, Time distribution diagram of floral visits to obtain nectar, morning returns from sleeping roosts, and evening returns prior to departing for sleeping roosts of *Sphex pensylvanicus* females.

given by Reinhard (1929) and Frisch (1938).

Nest enlargement.—Components of nest enlargement were as described by Reinhard (1929), Rau (1944), and Rigley and Hays (1977), including the manner of soil removal, except that females were unable to characteristically distribute the soil of the tumulus due to the vertical attitude of one nest and the space constraints imposed by the broken pieces of sewer tile of the other nests. Audible sounds accompanied nine nest enlargements. One wasp periodically made sounds for 56 min while enlarging her nest. Individual bursts of sound in this female lasted 1–5 ($\bar{x}$=3.1, N=18) min. These sounds evidently are a by-product of the wasps excavating with their mandibles in a hardened substrate. In this species, they may serve as an audible repellent to conspecific females attempting to gain access to pre-existing burrows (Rigley and Hays 1977).

Nest enlargement often occurred just prior to darkness. Four wasps that began enlarging nests after 1800 did not finish until well after 1900 hrs. Rigley and Hays (1977) noted that wasps dug as late as 2100 with most such activity occurring between 1100 and 1800 hrs.

Exits to sleeping roosts.—Females without prey returned in flight to nests between 1826 and 1948 hrs (Fig. 5), flew into the drain, entered the tile opening, and stayed inside 6–40 min ($\bar{x}$=23.8, N=26) before exiting. Such returns coincided with the sun beginning to disappear over a nearby hill and thus wasps returned to nests progressively earlier as daylength shortened. Some females arrived at the drain almost simultaneously, e. g., on 23 August 1981 two wasps arrived at 1844, 3 sec apart, and two others arrived at 1855, only 1 sec apart. By twilight, usually all but one or two of the females were inside burrows. Wasps then began leaving the drain by flying between the sewer grates, sometimes hesitatingly. The exit times of 22 females ranged from 1832 to 2008 hrs (N=100). After exiting, the wasps flew to their sleeping roosts, often on white sweet clover, 84 times without exhibiting any form of orientation. Seventy-eight (93%) of these exits were made by females that oriented previously that day. The wasps made air-borne orientation movements 16 times prior to flying to sleeping roosts. All of these flights were observed in females that made similar flights earlier in the day. Some females left, turned 180°, entered, and exited one or a few times, or occasionally circled once or twice, and then flew toward the sleeping roosts. Just as they flew to nests almost simultaneously, two pairs of females flew away only 3–5 sec apart on 23 August 1981.

DISCUSSION

Rigley and Hays (1977) noted that females of *Sphex pensylvanicus* used the same nesting site for at least three consecutive years by cleaning and renovating pre-existing conspecific burrows. In my study, females of this species reused 1980 burrows in 1981 and 1982. Twenty-one of 22 wasps utilized an enlarged common entrance and upper main burrow (broken drain tile) during these years. Use of pre-existing conspecific burrows by subsequent generations of wasps probably saved females considerable time and energy in excavation. The use of a common main burrow by more than one wasp and the reuse of burrows by siblings represent initial steps in the direction of semisocial behavior of aculeate Hymenoptera (Brockmann and Dawkins 1979).

Sphex ichneumoneus proceeds farther than this in preadaptation toward semisocial behavior. Burrows that are excavated and then abandoned by some females are adopted as useable nests by other wasps. The females adopting and renovating the nests of conspecifics save much time, often nearly two hours (Brockmann 1980), and energy that otherwise would have been unnecessarily invested in digging. Wasps that accidentally enter conspecific burrows evidently cannot distinguish between empty, abandoned burrows and those being actively provisioned (Brockmann and Dawkins 1979). Rarely, a female of *Sphex ichneumoneus* deposits a paralyzed katydid in a neighboring female's nest. The two wasps thus temporarily share the same burrow and cell. The intruder may even oviposit on a prey in the cell and fill the burrow, but eventually she returns to her own nest and finishes it (Brockmann and Dawkins 1979).

Sphex pensylvanicus incidentally may have evolved a behavior that lessens accidental intrusion into and takeover or sharing of conspecific nests. Rigley and Hays (1977) believed that sound produced by excavating females of this species acts as an auditory repellent to nest entry by conspecifics nesting nearby or investigating burrows. Females were often repulsed from entering nests in which previously taped, conspecific sounds were being replayed (Rigley and Hays 1977). Although they termed this sound "stridulation," implying in the classical sense of the definition that it was produced by two body parts rubbing together, it seems more likely that the sound was made as a by-product of the mandibles digging in a compact substrate. Such sound was produced intermittently by females adding side burrows and cells to their nests (pers. obs.).

Why do females of *Sphex pensylvanicus* return to their nests from sleeping roosts, feeding stations, or basking places each morning? The wasps could immediately begin searching for prey in the trees near the sleeping roosts and thus make better use of their time and energy. First, temperatures in the morning are too cool to facilitate searching for prey (see below). Second, females probably return to their nests every morning to examine the area for disturbance. Why waste valuable time and energy hunting, capturing and transporting prey if the nest has been destroyed or parasitized? Females probably also return to the nesting site each morning to reacquaint themselves with the surroundings in order to expedite subsequent returns to the nest with prey. More than half of the wasps made orientation flights upon returning to their nests the next morning.

Females of *Sphex pensylvanicus* spent, on average, more time inside nests following pre-darkness returns than after morning returns from sleeping roosts, feeding stations, or basking places, periodic inspection returns, or taking in prey unless engaged in subsequent nest enlargement. The shorter amount of time spent inside nests during midday may be related to increased temperature or absence of certain subterranean activities such as oviposition and burrow excavation.

About one-half of exits that followed morning or afternoon visits to nests progressed to orientation flights. In contrast, only one in three exits after placing prey in the nest and fewer than one in five exits following evening nest enlargement or pre-darkness returns and entries evolved into some form of orientation. The majority of wasps that did not orient following a visit to the nesting site either oriented previously following a morning return from their sleeping roost, feeding station, or basking place or subsequently fed on honeydew or nectar or basked in the sun instead of searching for prey. Certain wasps that did not orient following morning visits inside their nests had done so the previous evening. Other wasps that did not make an orientation flight may have done so earlier in the morning before I arrived at the study site. Change in temperature may partly regulate the duration and extent of an orientation flight as the wasp's movements noticeably increased in rapidity with increased temperature during midday.

Although orientation flights have been described for a number of sphecid species (Evans 1966), few authors conclusively ascertained the function(s) of these flights. Tinbergen (1932, 1935) and some of his colleagues probably came closest to ascribing a specific function to them, that of familiarization with landmarks in the vicinity of the nest to facilitate subsequent provisioning activities. In *Sphex pensylvanicus* the purpose of orientation flights seemingly is to acquaint or reacquaint the female with her surroundings, but as the sallies of some wasps extended a great distance (>13 m) from the nesting site it was difficult to separate the final stage(s) of such flights from the longer (55–60 m) flights to the hunting ground. By familiarizing herself with her immediate environs, a female probably facilitates an expeditious straight-line return to the nest with a large and heavy prey. Otherwise, much time and energy would be expended in aerially searching, more or less at random, for the nesting site.

Orientation flights in *Sphex pensylvanicus* were observed only in conjunction with an active nest. They usually decreased in duration and complexity as the wasps made successive trips to and from their nests. Females usually flew to the nesting site with prey from the direction in which they made orientation sallies and left. Females became disoriented upon their return when foreign objects or obstacles were placed near the storm sewer drain cover. If orientation flights served for parasite avoidance rather than reconnaissance (McCorquodale 1986), as one anonymous reviewer suggested, then shouldn't they be made while transporting prey to the nest rather than when exiting it?

Weather clearly influenced the nesting and provisioning activities of females of *Sphex pensylvanicus*. Wasps did not appear at the nesting site on rainy or excessively overcast days. However, on cloudy mornings, females appeared at the nesting site usually within 1 hour after the cloud cover had dissipated. Females arrived at their nests from sleeping roosts on cool, sunny mornings as early as 0635 hrs at an air temperature as low as 10°C. Wasps provisioned their nests with katydids at air (shade) temperatures as high as 33°C.

Certain activities of *Sphex pensylvanicus* females regularly occurred from midmorning through the afternoon, and, in the case of orientation flights and prey transport, into early evening (Fig. 4). Orientation flights preceded or followed many wasp activities and, although somewhat bimodally distributed around the hottest period of the day, were observed from 0859 to 2004 hrs. Periodic visits to nests, also somewhat bimodally distributed around the hottest hours of the day, began at 0934 but were not seen after 1638 hrs probably because females were feeding on honeydew or nectar, basking in the sun, or searching for prey after that time. Provisioning flights were seen interspersedly from late morning (1032 hrs) to early evening (1924 hrs) on sunny days, except for around the noon hour (EST). They were evidently temperature regulated, as they occurred only between 23 and 33°C peaking at 27–29°C. Provisioning times (1030–1300, 1400–1500, 1630–1900 hrs) were sandwiched around times when the wasps were either feeding, basking in the sun, or undertaking some other activity.

In contrast to the somewhat broadly but bimodally distributed orientation flights, periodic visits to the nesting site, and prey transport flights, morning returns to nests from the sleeping roosts and arrivals at the nests before dusk followed by departures for sleeping roosts were strongly pulsed because of the specific functions of these activities (Fig. 5). Flights from sleeping roosts to nests occurred only from 0635 to 1038 hrs and returns to sleeping roosts near dusk took place only between 1832 and 2008 hrs. The latter behavior seemed to be highly synchronized because conspecifics sometimes both arrived at the nesting site and departed from it in pairs only one or a few seconds apart. Feeding on the nectar of flowers was mildly bimodally distributed (1100–1200, 1400–1700 hrs) during late morning and mid- to late afternoon. Such synchronized feeding could have been governed by temperature, light intensity, and/or nectar availability.

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LITERATURE CITED

Belavadi, V. V. and P. Mohanraj. 1996. Nesting behaviour of the Black Digger Wasp, *Sphex argentatus* Fabricius 1787 (Hymenoptera: Sphecidae) in south India. *Journal of Natural History* 30: 127–134.

Bohart, R. M. and A. S. Menke. 1963. *A Reclassification of the Sphecinae with a Revision of the Nearctic species of the Tribes Sceliphronini and Sphecini (Hymenoptera, Sphecidae).* University of California Press, Berkeley. 181 pp.

Bohart, R. M. and A. S. Menke. 1976. *Sphecid Wasps of the World. A Generic Revision.* University of California Press, Berkeley. 695 pp.

Brockmann, H. J. 1980. The control of nest depth in a digger wasp (*Sphex ichneumoneus* L.). *Animal Behaviour* 28: 426–445.

Brockmann, H. J. and R. Dawkins. 1979. Joint nesting in a digger wasp as an evolutionary stable preadaptation to social life. *Behaviour* 71: 205–245.

Evans, H. E. 1966. The behavior patterns of solitary wasps. *Annual Review of Entomology* 11: 123–154.

Frisch, J. A. 1938. The life-history and habits of the digger-wasp *Ammobia pennsylvanica* (Linn.). *American Midland Naturalist* 19: 673–677.

Krombein, K. V. 1955. Miscellaneous prey records of solitary wasps. I. (Hymenoptera: Aculeata). *Bulletin of the Brooklyn Entomological Society* 50: 13–17.

McCorquodale, D. B. 1986. Digger wasp (Hymenoptera: Sphecidae) provisioning flights as a defence against a nest parasite, *Senotainia trilineata* (Diptera: Sarcophagidae). *Canadian Journal of Zoology* 64: 1620–1627.

Rau, P. 1944. The nesting habits of the wasp, *Chlorion (Ammobia) pennsylvanicum* L. *Annals of the Entomological Society of America* 37: 439–440.

Reinhard, E. G. 1929. *The Witchery of Wasps.* Century Company, New York. 291 pp.

Rigley, L. and H. Hays. 1977. Field observations including acoustic behavior of the Black-Digger Wasp, *Sphex pennsylvanicus* (Linn.). *Proceedings of the Pennsylvania Academy of Science* 51: 32–34.

Ristich, S. S. 1953. A study of the prey, enemies, and habits of the Great-Golden Digger Wasp *Chlorion ichneumoneum* (L.). *Canadian Entomologist* 85: 374–386.

Tinbergen, N. 1932. Uber die Orientierung des Bienenwolfes (*Philanthus triangulum* Fabr). *Zur Vergleiche Physiologische* 16: 305–335.

Tinbergen, N. 1935. Uber die Orientierung des Bienenwolfes. II. Die Bienenjagd. *Zur Vergleiche Physiologische* 21: 699–716.