

The Stubborn Tenacity of Female *Sphex pensylvanicus* Linnaeus, 1763 (Hymenoptera: Sphecidae) with Their Prey¹

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Abstract: An aggregation of *Sphex pensylvanicus* nesting in soil behind a retaining wall on a residential lot in Sioux City (Iowa, USA) was observed over fifteen years. Many encounters of carriage of paralyzed prey (katydids) are reported, and instances when the prey was taken from the wasps are discussed.

Key Words: *Sphex pensylvanicus*, Hymenoptera, Sphecidae, prey carriage, katydids, Tettigoniidae, Sioux City, Iowa, USA

Introduction

The Great Black Wasp, *Sphex pensylvanicus* Linnaeus, 1763 is a large (20–35 mm long), solitary fossorial wasp. The females hunt katydids (Tettigoniidae) which they paralyze with a venomous sting and then store in underground cells as still-living food for their larvae. I reviewed the literature, listed the hitherto reported species of katydids known to have been hunted by *S. pensylvanicus* (Lechner 2016), and added confirmed prey species of katydids from the aggregation on my residential lot (Lechner 2016, 2017).

Nearly a century ago, E. G. Reinhard and Father J. A. Frisch, S.J. jointly made observations of *S. pensylvanicus* (as *Ammobia pennsylvanica*) nesting inside greenhouses on the grounds of Woodstock College, Woodstock, Maryland. They published separate accounts of their observations on the Great Black Wasp (Reinhard 1929, Frisch 1938) in which they disparaged the abilities of *S. pensylvanicus* to overcome any obstacles in their efforts to store their prey katydids in burrows. A few quotations exemplify their attitudes [words/phrases inside square brackets added by me for clarity].

“Three times a wasp bumped into me, dropped her Katy [katydid, Orthoptera: Tettigoniidae], and did not come back for it.” (Reinhard 1929)

“It was evidently difficult for the wasp to alter the course of her flight on short notice. Repeatedly, the burdened wasps crashed into me when I was on

¹ Received on January 27, 2022. Accepted on February 2, 2022. Last revisions received on February 19, 2022. Although the correct spelling of the US state is Pennsylvania (with two consecutive “n”), the correct spelling of the species is *Sphex pensylvanicus*, not *Sphex pennsylvanicus*.

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the line of flight to their burrows. At such times they always dropped their prey and abandoned it.” (Frisch 1938)

Frisch and Reinhard plugged the entrances to three burrows in the chinks between the granite blocks comprising a vertical wall inside a green house and did not return for several days. Upon return, they found 252 katydids lying in a heap on the floor below the plugged burrows. Reinhard (1929) wrote,

“What dogged persistence, what stupidity too, these three wasps exhibited. They kept right on hunting and bringing home prey to burrows they could not enter. Repulsed each time at the entrance, they dropped their booty, and, undaunted, sallied off for more.”

Frisch (1938) stated that

“The wasps, whose entrance tunnels were in the crevices between the rocks of the retaining walls, more often than not, dropped their prey in attempting the difficult feat of landing on the vertical wall and entering their tunnel with the dangling, long-legged katydid. Never once did I see an attempt made to recover the lost prey. Instead the wasps returned to their hunting almost immediately. This fact afforded an opportunity of testing the wasp’s ability as a huntress. Three of the tunnels in the retaining wall, all within the radius of one foot [~ 30.48 cm], were plugged tightly. Five days later, a total of 252 katydids had been brought in and dropped by these wasps, an average of 16.8 katydids per wasp per day, a monument to the wasp’s stupidity as well as to her prowess as a huntress.”

A more recent paper (Rigley and Hayes 1977) also mentions female *S. pensylvanicus* nesting in a vertically oriented colony in a riverbank in Maryland.

“If the prey was dropped following a collision with the bank or during climbing, it was never picked up and the female would leave.”

Given the above comments, I am compelled to report some of my observations of this wasp and its prey from an aggregation that had been nesting in the soil behind a vertical retaining wall on my residential lot in Sioux City (Iowa, USA) for at least 15 years. And, with few exceptions, the females here were found to be quite relentless in their efforts to recover their katydid prey and store them in their nests. As should become apparent subsequently, the female *S. pensylvanicus* in my aggregation seemed anything but "stupid".

Methods

The observation site was my residential lot in Sioux City (Iowa, USA) and a concrete block and railroad tie vertical retaining wall running along the north lot line was the location of an aggregation of *S. pensylvanicus* through 2017. I had been watching the activities of these wasps over the years and have made over 2,000 sightings. Observational methods have varied. Sometimes, I would sit in one spot and watch the wasps for hours; other times I only made sporadic checks at the wall. Wasps were sometimes marked with unique identification – multiple dozens of wasps in some years – in others, only a handful or fewer. For a detailed description of the nesting aggregation site including how wasps were marked for identification, the reader is referred to Lechner (2022). But whether marked or unmarked, female wasps were seen bringing their prey katydids to be stored in the soil behind the retaining wall.

Results

I counted 161 instances of female *S. pensylvanicus* bringing katydid prey to the wall. In some cases, I only saw a wasp swiftly flying past me as she flew her katydid into her wall entryway. In such a situation, the observation time was less than a second, and I only knew she had a katydid by a glimpse of the prey's bright light green color. Other sightings were of a much longer duration as will become evident shortly. Wasps brought their prey to their nests throughout the day, but most prey carriage events were clustered past midday as shown in the histogram below (Figure 1).

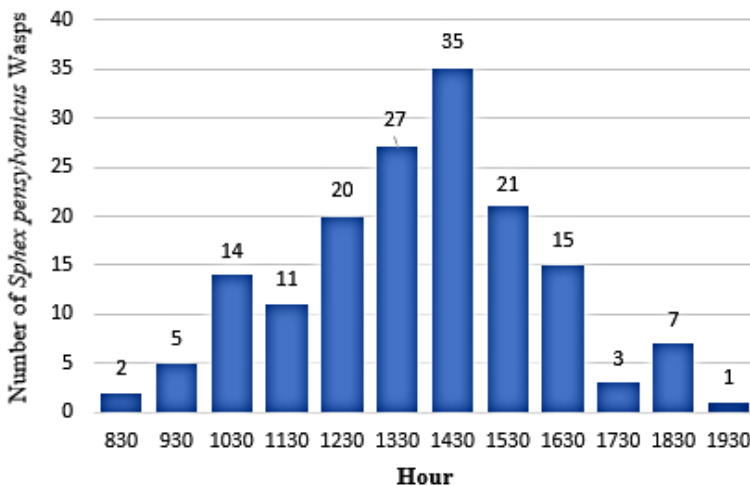


Figure 1. Histogram showing distribution of prey carriage by *Sphex pensylvanicus* by times of day. 2003 – 2017. Each number represents the midpoint of the corresponding time period. For example, 830 is the midpoint of 8:00 to 8:59AM, etc.

The prey having been previously stung by the wasps are still alive but are paralyzed by the venom yet are not entirely immobilized. As described by previous authors, stung katydids can exhibit gentle movements of their antennae, mouth parts and rhythmic pulsations of the abdomen including passing fecal pellets (Reinhard 1929, Frisch 1938, Kurczewski 1997). I can confirm the same condition of stung katydids brought in by the wasps at my aggregation (Table 1).

Table 1. Observations of a Paralyzed Katydid Nymph (? *Microcentrum* juvenile) from 7 August to 23 August 2004.

Day in August 2004	Time	Observations					
		No. Fecal Pellets	Movement				
			Palpi	Head	Antennae	Legs	Abdomen
8	9:25	6					
	15:12	2					
	16:45	1					
9	16:40	3					
10	10:12		X				
11	9:00		X		X		X
12	16:25	1	X				X
13	8:15		X				
15	9:15	1	X				
16	7:15	1					
17	7:40		X				X
18	7:50		X				X
19	7:30		X			X ¹	
20	7:30		X	X		X	
21	7:15		X			X	X
22	7:45		X	Brownish discoloration on thorax			
23	16:45	Nymph now unresponsive – discolored - sacrificed					

1. Tarsus of right middle leg.

Referring to the descriptions of both Frisch and Reinhard at their aggregation of *Sphex pensylvanicus*, indications are that the wasps could tolerate no obstacles in their flight path to their nest entrances. I never saw such problems with the *S. pensylvanicus* in my aggregation. In one case a prey-laden wasp flew directly over me as I was sitting at my observation post, crashed into the side of the house, and then, without dropping her katydid, flew directly into her entrance in the retaining wall (25 August 2003).

In another episode, I had moved a plywood box directly in front of two openings in one of the blocks in the wall thereby completely altering the appearance of this small portion of the wall (5 August 2003). About two minutes later, an *S. pensylvanicus* flew directly to this location and without the slightest

hesitation went behind the box via the very narrow gap between the box and the wall and entered. This wasp seemingly needed no apparent visual cue whatsoever to know where her entry point was located.

After 2003, I devised a system whereby the entrances into the north lot line retaining wall could be securely blocked thus denying the wasps access into the wall unless I removed the impediments. Of 161 prey carriage observations, there were 91 times when the wasp's entry was blocked. I would then approach the wasp as she still held onto her prey. Sometimes she would be sitting on the vertical surface of the wall or land in the lawn near the base of the wall below her intended entryway. Other times she would remain in near-hovering flight in the same area. Of the 91 times, I was able to take the katydid away from the wasp 56 times. If my close approach did not startle the wasp into dropping her prey, I could sometimes catch hold of the prey right at the wasp's wall entryway and pull it away from her or swatting it out of her grasp and picking it up. On those occasions, I would try to hold the katydid loosely but securely in my fingers -dorsum upward and head forward - and present it toward the wasp as she was making short, quick, agitated darting hovers and facing in my direction as if she were evaluating me and this situation. How would she respond to my theft? Would she try to retrieve it from me or just ignore me and fly away as predicted by Frisch and Reinhard?



Figure 2. *Sphex pensylvanicus* flying to my hand and just getting ready to land on my fingers. I shook the wasp from the prey which I then dropped to the ground. The wasp flew down and retrieved the katydid, but my attempt at grabbing the katydid again startled the wasp and she flew away. Prey item is an adult male *Scudderia furcata*. Photo taken 10 September 2013.

In just three of the instances, the wasp did fly away; and in another six cases, the wasp made a very perfunctory approach flight - short and quick, perhaps very briefly landing on my hand - to the katydid but then flew away. However, all the other times the wasps made vigorous attempts to retrieve their prey from my grasp. The wasp would fly to my hand (Figure 2), align herself to the katydid's body head-to-head in a dorsal straddle position in order to grasp the katydid's antennae (Figure 3) and then grab on (Figures 4 and 5). In cases like that, the wasp would begin vigorously beating her wings to initiate flight (Figures 6 and 7). If not held too tightly, the wasp would tear her prey from my grip and, if I had removed the blocking impediment at the beginning of the episode, would fly with her prey directly and unhesitatingly into the wall opening in most cases.



Figure 3. *Sphex pensylvanicus* orienting herself and getting ready to straddle the katydid and grasp by the base of the antennae. As my grip was fairly tight, the wasp gave up her retrieval attempt in less than a minute and flew away. Prey item is an adult male *S. furcata*. Photo taken 17 August 2011.



Figure 4. *Sphex pensylvanicus* straddling her prey using her front legs and mandibles to hold the katydid. The wasp successfully retrieved her prey and flew it into her nest entryway. Prey item is an adult male *S. furcata*. Photo taken 28 July 2011.



Figure 5. *Sphex pensylvanicus* holding her prey using the same technique as in Figure 4. Wasp successfully retrieved her prey and stored it. Prey item is a *Microcentrum* juvenile. Photo taken 30 July 2011.



Figure 6. *Sphex pensylvanicus* beating her wings to remove prey from my grip. Prey successfully retrieved and stored. Prey item is an adult *S. furcata*. Photo taken 6 August 2011.



Figure 7. Another *S. pensylvanicus* attempting to fly her katydid away from my grasp. Prey was taken away from this wasp twice which she retrieved twice then successfully took prey into the wall. This was wasp #16 from the 2012 season and can also be seen in my previous paper on long distance homing flight challenges (Lechner 2015, Figure 1). Prey item is an adult *S. furcata*. Photo taken 21 July 2012.

On an even more amazing note, there were times when I had not removed the blockage in the wall, and the wasp flew her prey back to the wall in a continuing attempt to store the prey. I would again steal the prey from the wasp. A most remarkable such episode occurred on 5 September 2013. On that date, a wasp flew to the wall with prey, an adult female, possibly *S. furcata* (species not authoritatively determined - the same for all katydids discussed in this paper - refer to Acknowledgements), and finding her entryway blocked was unable to enter. I was able to take the katydid away from her. The wasp immediately made a prey retrieval attempt as I held the katydid. I then carried both wasp and prey to an area, a concrete patio, where my clear view of the substrate would be unimpeded. With a vigorous shake of the wrist, I dislodged the wasp (which all this time was still struggling to retrieve her prey) and dropped the katydid to the patio. The wasp quickly flew down, retrieved her prey, and took off, flying directly back to the retaining wall. With entryway still blocked, I stole the katydid again. The wasp attempted retrieval, and again I took the wasp and her prey to the patio. With another vigorous shake, I dislodged the wasp and dropped the katydid to the patio.

This time when the wasp flew down to retrieve her prey, she straddled it while still on the patio and rested for at least a full minute before climbing, with prey, up onto my shoe then quickly with wings beating furiously walking up my pant leg to thigh height. At this point she took flight with the prey going directly to the wall. Again, with the entryway still blocked, I stole the katydid away from this wasp for a third time. The wasp at once began the process of retrieving the katydid, and I repeated the procedure of shaking her loose and dropping the katydid to the substrate. Now, however, the wasp apparently had wearied of this back-and-forth game and made no attempt to look for her katydid and flew away.

Wasps will apparently ascend any vertical surface to gain height before flying with prey. Dow (1932) described an incident in Cuba in which *Chlorion (Ammobia) cubensis* Fernald, 1906 was dragging an adult female katydid, *Neoconocephalus maxillosus* (Fabricius, 1775), up a tree trunk, and also similar behavior by *Sphex speciosus* (Drury, 1773) carrying a heavy cicada up a tree to gain height. Balduf (1941) wrote of his observations of a large black wasp that was vertically ascending a wooden porch post while carrying an adult tettigoniid orthopteran as well as a *S. speciosus* with prey climbing from ground level up his shoe, trouser leg, and all the way to the top of his head before taking flight. In addition to my previous incident in September 2013 described above, I had four more encounters with a prey-laden *Sphex pensylvanicus* climbing on me to gain elevation. Examples are shown in Figures 8 and 9.



Figure 8. *Sphex pensylvanicus* has retrieved her prey from the substrate where I had set it. She then climbed with the katydid up onto my shoe. Prey item is an adult *S. furcata*. Photo taken 4 September 2013.



Figure 9. *Sphex pensylvanicus* after having retrieved her prey from the ground began climbing my pant leg to gain height before flying off. I took the prey from the wasp twice and each time she climbed my pant leg. I let her enter the wall with the katydid after her second retrieval. Prey item is an adult *S. furcata*. Photo taken 1 September 2013.

Finally, how long do these prey retrieval episodes take? It was quite variable depending on how many times I took the prey away in an individual episode. For example, on 17 August 2008, I took an adult *Neoconocephalus* away from a *S. pensylvanicus*, and from the time I presented the prey back toward the wasp until she retrieved it from me and flew it into her wall entryway was probably less than five seconds.

The prey retrieval episode that occurred on 11 August 2017 took somewhat longer, and with the demise of my *S. pensylvanicus* aggregation after the 2017 season, was my final encounter with a prey-laden *Sphex pensylvanicus*. In this instance, I had a stopwatch and activated it when I saw the wasp with an adult female *S. furcata* trying to enter her entryway which was blocked. My closer approach startled the wasp, and she dropped her prey which I picked up immediately and presented to her. She retrieved the katydid from my hand, flew it to the still blocked entry, and dropped it again when I moved in too close. Again, I picked it up, presented it to the wasp, and she retrieved it again and flew it back to the blocked entry. This time the wasp altered her behavior and flew south and east over the backyard, yet I could see she still held on to her prey as she eventually flew out of sight. I did not remain in the area awaiting her return, so I don't know if she had given up completely. This entire episode was timed by stopwatch at 3 minutes 41 seconds.

It would not have been beyond the realm of possibility that the wasp returned with her prey shortly thereafter. I saw one such instance on 2 September 2009. On that date I noted a wasp that I had previously marked with a spot of white paint with an adult *S. furcata* resting on the vertical surface of the north lot line retaining wall by her blocked entryway. I took the prey from her and then presented it back toward her direction. The wasp quickly retrieved the katydid from me, but instead of flying into the now opened entryway, she flew away behind me and out of my line of sight. In about one minute the wasp (easily recognized by her paint spot) returned with her katydid and flew directly into her entry. This wasp was also one of the subjects in a previous paper (Lechner 2016, see Figures 6, 7, and 8).

Although not one of my prey theft attempts, the episode described below is among the best observed examples of the tenacity of female *Sphex pensylvanicus* and their instinct to hold onto and store their prey. At approximately 10:25 a.m. on 14 August 2017, I saw the wasp designated as "Brown" (for the color I had previously painted on her scutum) fly to the railroad tie portion of the north lot line retaining wall with her prey, an adult female *S. furcata*, and attempt to enter the wall. However, I had blocked her area of interest tightly beforehand with some cloth rags. Activating my stopwatch upon her arrival, I observed as "Brown" struggled in vain to bypass the cloth blockage for 5 minutes 39 seconds. At this time, "Brown" flew away, southward, with her prey two houses farther down from my lot until she was no longer in sight. Yet, about a minute later,

"Brown" flew back with the prey, presumably the same katydid she had been carrying before, and again tried to get into the wall past the blockage. I timed this second attempt at 1 minute 18 seconds. I was then apparently too close for her comfort, and the startled "Brown" dropped her prey and flew away ending this episode.

Discussion

Given my experiences over a fifteen-year period with female *Sphex pensylvanicus* and their prey, I am at a loss to account for the observations of Frisch and Reinhard. Certainly, I am reluctant to attribute "stupidity" to the wasps in the aggregation I watched contrary to what Frisch and Reinhard attributed to theirs at their Maryland location. These two gentlemen had blocked their wasps' burrow entrances and then left their aggregation alone and unobserved for five days. I, on the other hand, actively interfered with my wasps and their prey transport multiple dozens of times. Perhaps if I had only blocked the wall entrances and left the wasps undisturbed maybe I too would have seen hundreds of paralyzed katydids lying at the base of the wall. I cannot attempt this experiment since the *Sphex pensylvanicus* aggregation in my north lot line retaining wall has been extinct since 2018.

Acknowledgements

Although none of the katydid species discussed in this paper were identified by experts in the Tettigoniidae, I based my identifications on previously collected specimens that had been authoritatively determined. In this regard, I extend my wholehearted thanks to Dr. Thomas J. Walker, Professor Emeritus, Department of Entomology and Nematology, University of Florida, Gainesville, Florida, and curator of their Ensifera collection, who identified the katydids discussed in my previous papers (Lechner 2016, 2017). I am in debt to Dr. Walker, his field guide (Capinera et al. 2004), and his many e-mail communications to me over the years for the knowledge I have gained on katydids.

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