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The mechanism of prey capture and mass provisioning by the Nigerian solitary wasp (*Sceliphron servillei*) (Hymenoptera: Sphecidae).

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ABSTRACT

A study was conducted to investigate the basic physiological factors that tend to guide the Nigerian solitary wasp *Sceliphron servillei* in its mass provisioning behavior in Sapele, Nigeria. This was done both in captivity and in the wild. In the wild, ten sealed cells were reopened and the immobile spiders counted and measured. To ascertain what prompts the wasp to lay eggs and seal the nest, one of the spiders was pulled out to the entrance of cells that were being provisioned. The carrying capacity of each cell was also determined by measuring the diameters as well as their depth. A cuboid-shaped insect cage; furnished with a dish of wet mud, two potted plants to create a natural environment and a dish of dilute honey to nourish the solitary wasps was used to study the mud-daubers in captivity. Five gravid and active female wasps were caught and released into the cage. Finally orb-web spinning spiders were incrementally released into the cage. The number of spiders per cell bears no correlation with the internal surface areas (ISAs) of the cells ($p < 0.05$) although the ISAs of the cells were significantly the same ($p > 0.05$). Larger spiders were few while smaller ones were many per cell. The wasps were found to seal up the cells (even without laying eggs) with only two spiders when one of them was drawn to the entrance indicating that volumetric capacity of the cell can trigger off the instinct to do so. In captivity, the wasps only began to build nest when the prey population peaked. Large spiders received multiple stings and large dose of venom while opposite is the case with the smaller ones. Spiders that die from overdose during hunting were dropped and not flown to the nest for provisioning.

Keywords: Mass provisioning, Internal surface area (ISA), venom, Sting, Spider. Nest cell.

1. Introduction

Elegant in appearance and distinctive in their actions, solitary wasps have long fascinated observers and have been the subject of narratives by naturalists and scientists (Kelvin 2001). Wasp is typically defined as any insect of the order Hymenoptera and suborder *Apocrita* that is neither a bee nor ant. The majority of wasp species (well over 100,000 species) are "parasitic" (technically known as parasitoids). Their ovipositors are used simply to lay eggs, often directly into the body of the host. The most familiar wasps belong to *Aculeata*, a division of *Apocrita*, whose ovipositors are adapted into a venomous sting, though a great many aculeate species do not sting, (Norman and Triplehorn, 2004).

There are many species of sphecid wasps. Most are shiny black or metallic blue, some with bright red, yellow, or orange markings. The most common sphecid wasps are in the subfamily Sphecinae and are called "Thread-Waisted Wasps." Some sphecids, often called "mud-daubers," make mud nests for their larvae which they attach to the sides of rocks and buildings (O'Neil, 2001 & Ward *et al.*, 2002). All adult solitary wasps are fertile. They generally live and operate alone, and most do not construct nests. The nesting habits of solitary wasps are more diverse than those of social wasps. Mud daubers and pollen wasps construct mud cells in sheltered places typically on the side of walls. Potter wasps similarly build vase-like nests from mud, often with multiple cells, attached to the twigs of trees or against walls. A single egg is laid in each cell, which is sealed thereafter, so there is no interaction between the larvae and the adults, unlike in social wasps, (O'Neill, 2001 and Katja & Blake, 2007).

Solitary wasps and parasitic wasps are an important component in a variety of ecosystems: almost all solitary wasp species provide insects or spiders to their larvae, either by laying their eggs in burrows provisioned with prey or by laying their eggs inside insect hosts. Most species are very specific about the types of prey that they hunt. Mud-daubers, for instance, pack their mud tubes with spiders. The egg hatches and the larvae consume the supplied food without

ever leaving the cell. After pupation the new adults emerge, seek a mate after which the males being shorter lived in most species die and the females go on to restart the cycle (Elgar & Jebb 1999 and O'Neill 2001).

An intensive survey was conducted on the Nigerian solitary wasp *Sceliphron servillei* both in the wild (natural environment) and in captivity. The aim was to study this insect at close quarters and to ascertain some basic physiological factors that tend to guide the insect in its mass provisioning behavior.

2. Materials and Methods

This study was carried out in Sapele and its environs in Delta state, Nigeria. Sapele is one of the major cities in the Niger Delta zone of Nigeria. It shares a dual vegetation belt – the swampy forest and the rainforest. It has two climatic seasons– the dry season and the wet season with maximum rainfall in May or June and again in October. Although no month is completely dry, there are two relatively drier periods between December and February and between July and September.

The Nigerian solitary wasp-*Sceliphron servillei* was studied both in the natural environment and in captivity. The study was conducted in the dry season-between November and February. Experience has shown that the nest is vulnerable to water. Few drops of water would not only cause the sealed nest to disintegrate into muddy particles but also tamper with the developmental processes of the larvae and pupae; depending at what stage of larval or pupal development the wetness took place (Ighere, 2004).

2.1 In the Wild

Ten different nestling sites were randomly sampled out for a close up survey. Potential nestling sites included rest rooms, eaves of ceiling, uncompleted but roofed houses, walls of sitting rooms, suspended but non-functional electric bulbs and ventilation openings of houses. In each nestling site, the solitary wasp was observed right from when it plastered the first wet mud until it sealed the cell after provisioning it and laying its egg on the prey.

First, ten sealed cells were reopened and the immobile spiders counted and their sizes compared. Secondly, the time during provisioning at which each of the studied wasps lays its egg on the prey was observed. To ascertain what prompts the wasp to lay eggs and seal the nest, we picked out five cells from different sites which have just been provisioned with only two spiders. In each case one of the spiders was pulled out to the entrance of the nest chamber awaiting the arrival of the wasp which has gone hunting for more prey. To ascertain the carrying capacity of each cell, the diameters as well as the depth of the almost cylindrical cells were measured. To compute the internal surface area (ISA), the total value was halved because the *Sceliphron* cell is not a complete cylinder longitudinally. They are always like a carrot cut in halves longitudinally.

2.2 In Captivity

A cuboid-shaped insect cage was constructed and used to study the insect in captivity. The dimension of the insect cage was 63 cm by 43.5 by 35 cm. This gave an approximate internal surface area of 94.82 m². Wooden beams were used to construct the structure. The entire cage except the floor was wrapped with a fine-meshed mosquito net. A carton material was used to reinforce the edges and carpet the floor. A thermometer was fitted into the cage from above to monitor the internal temperature.

The cage was furnished with a dish of wet mud to provide material for nest construction, two potted plants to create a natural environment and a dish of honey diluted with distilled water to nourish the solitary wasps. The mud and potted plants were watered every other day with the aid of a 2 mm wide nozzle fitted to a dropping can. The honey dish was renewed every four days to avoid microbial growth and possible contamination. The door to the cage was constructed at one end of the cage with a loose mosquito net that was always knotted when not in used. The cage was placed on a table close to a wide window in the laboratory. It was placed in such a way to allow both ample ventilation and sunlight into the cage.

Table 1: The depth and diameter of the Nigerian solitary wasp (*Sceliphron servillei*) nest cells.

Cell	Depth(mm)	Diameter Before Oviposition (mm)	Internal Surface Area (ISA) (mm ²)	The Number Of Spiders Per Cell
A.	27	6	381.9	9
B.	27	7	519.8	14
C.	27	7	519.8	6
D.	30	7	577.5	8
E.	27	7	519.8	15
F.	25	7	481.3	5
G.	27	7	519.8	7
H.	26	7	500.5	4
I.	27	7	519.8	3
J.	27	7	519.8	6
Total	270	69	5060	77
Mean	27	6.9	506.0	7.7

Five gravid and active female wasps were caught and released into the cage. Catching them was easy. We searched out and stood around different nestling sites where nest construction was in progress. Each wasp was captured as it tries to put a finishing touch to the interior of a cell under construction. To do this they usually

enter the nest head-first and spends some few seconds within; oblivious of the outside world. It is at this point a 2 mm wide test-tube is inverted over the cell. Being so agitated, they usually back out into the test-tube which was eventually withdrawn and stuffed with cotton wool. In this manner, each gravid species of the

Sceliphron servillei was captured and transferred to the cage. Twenty four hours were given to the ‘captive wasps’ to acclimatize to the new environment.

The next stage was to release orb-web spinning spiders into the cage. This was done incrementally until the cage was heavily populated with different species of spiders. The events that followed such as nest construction, prey hunting and prey capture mechanism were observed and documented.

3. Results

In the Wild

The depths and diameters of the cells built by the different mud-daubers were significantly the same ($p > 0.05$). The details of the collected data are shown in table 1. The average depth and diameter were 27 mm and 6.9 mm respectively. The internal surface areas of the sampled cells were also significantly the same. Although cell A (381.9 mm^2) and F (481.3 mm^2) differed, from the other eight cells which were greater than 500 mm^2 .

The number of spiders scooped out of the already sealed cells differs both in numbers and sizes per cells. Cell E (ISA = 519.8

mm^2) has the largest number of spiders which is fifteen. Note that cells B, C, G, I and J with similar ISAs had different numbers of spiders which are 14, 6, 7, 3 and 6 respectively. It is also worthy of note that cell A with the smallest ISA (381.9 mm^2) has 9 spiders while bigger ones such as cells H (ISA = 500.5 mm^2), F (ISA = 481.3 mm^2) and I (ISA = 519.8 mm^2) had fewer numbers which are 4, 5 and 3 respectively. The range of spider content between the cells stood at 12 (that is 15 – 3).

The spiders scooped out of the various mud dauber cells differ significantly in sizes ($p < 0.05$). Except for those that have been devoured by the first instar larvae, all the spiders scooped out showed signs of life. When touched with a pick stick, they do move one or two legs. It was observed that the smaller they were, the more they are per cells. The bigger ones fill the cells easily and are thus fewer in number. Figure 1 shows a nest cell from which different spiders have been scooped out. It also showed web-weaving spiders of different sizes scooped out of some cells. The two white specks attached to two of the spiders were eggs laid by the mother wasps before sealing up the cells. In the lower session of the picture are two larvae in their third and fourth instars.



Fig 1: Spiders scooped out of the cells belonging to the Nigerian solitary wasp *Sceliphron servillei*



Fig 2: A cocoon extracted from one of the wasp cell containing an advanced pupa

Observation showed that the mud dauber wasp laid their eggs on the third or fourth spider from within. When dealing with large spiders, the eggs were laid on the second prey before sealing up the cell. To lay their eggs; the wasp were observed to enter the cell gaster-first instead of the head. The time duration for the laying of the egg was in less than thirty seconds after which they flew off to hunt for more prey and complete the provisioning.

A spider-filled cell was found to elicit the instinct to stop provisioning and seal the cell. It was observed that each of the wasps dropped its spider when it returned and found a spider at the entrance of the cell. As if this was not expected, the mud-dauber was observed to pause for a brief moment all the while roaming over the entrance of the *filled* cell. It eventually dropped the load of prey, flew off only to return with a ball of wet mud for sealing the cell. The sealing up process was always simple and brief. It involved a ball of wet mud being deposited at the entrance of the cell and then smoothing it over with the mandibles. After which the mud-dauber flies away on the premise that the cell has been fully provisioned and that a fertile egg has been laid within the cell. In all the studied cases, no egg was laid before the cell was sealed up and abandoned by the solitary wasps.

In Captivity

The studied solitary wasps were able to survive in the cage for the three weeks period in which the study was conducted. The diluted honey meal was able to sustain them. They acclimatized to the new environment with unexpected ease. Within an hour they began to move, fly and buzz about within the cage after some moments of motionlessness. They showed no aggression.

Initially, there were no moves to begin nest construction. However, as the population of spiders increase in the cage, the first sign of nest construction began. The restlessness among the 'captive wasps' as more spiders were supplied was significant. They flew and buzzed about within the cage, picked up mud, selected one of the wooden poles and plastered their first mud. Three of the five wasps were observed to build nests while the other two flew restlessly about without picking up a single construction mud.

Only few of the spiders climbed the potted plants. A great majority of them scurried to hide themselves behind the wooden poles. Those that dare climb the potted plants hid themselves under the leaves. None of them spun a silky web. The hunting process was fascinating. Two types of flight pattern were observed during the prey hunting process. The first involved a sluggish buzzing flight which is seemingly designed to agitate and stir the prey. The end product of this was that the hiding prey was searched out and located. The second flight was silent and quick. In a quick dash and like a lightning the wasp pounced on the prey and grabbed it. Seized by the mandibles and held in place by the pro-thoracic legs, the wasp positioned itself with the aid of the long meta-thoracic legs. Curling the flexible petiole ventrally inward, the predator wasp ejected the sting which is at the end of the menacing gaster. In a flash the sting was drilled into the struggling prey. A brief moment was given to the spider to go limp as felt by the wasp. In some observed cases, more struggles by the prey invited more stings.

Observation showed that some spiders were stung just once and they went limp or became paralyzed and were immediately flown to the nest. Some others were stung two or three time before going limp. The stings were delivered at the intervals of five seconds. The time lapse before paralysis sets in was on the average of fifteen seconds. The sizes of the spiders seem to determine the number of stings they receive. A very big spider was stung five times in quick

succession before it went limp. Observation showed that not all the stung spiders were carried to the nest for provisioning. Those which were presumably dead were usually dropped and left without being carried to the nest. On being picked out, these leftovers were seen to be completely dead. They showed no signs of life such as moving of the legs and slight twitching of the body which the paralyzed ones usually exhibited.

4. Discussion

This study has shown that the Nigerian solitary wasp-*Sceliphron servillei* can be domesticated and studied in captivity. The experimental ones were able to survive on diluted honey syrup during the three weeks the study was undertaken in captivity. They were found to acclimatize easily. While in captivity they were not found to show any level of aggressiveness neither do they make any attempt to sting the researchers so long as they were not physically handled.

The study of the Nigerian solitary wasps in captivity had revealed that there is an inter-relationship between the predator (solitary wasp) and the prey population, (Blackledge and Pickett 2002). According to this study, the need to build nests and then hunt for prey began when the population of the spiders was maximally increased in the cage. Predator-prey population dynamics is an old ecological phenomenon. Other studies have confirmed that both populations show cyclical behavior, and that the predator population generally tracked the peaks in the prey, (Begon *et al.*, 1996 and Gotelli 1998). The Nigerian solitary wasps had shown that the instinct to embark on a major life activity such as reproduction and hunting for prey can be driven by a high prey population. Closely related to this is the hunting technique. The sluggish buzzing flight was observed to stir the prey for the wasp to acquire its target. Then, just like the prowling lion, the hunting wasp silent in a silent and quick flight.. These hunting techniques exhibited by most predators. The wasp like every predator no doubt has mastered this predatory instinct over the years.

The study has also revealed the number of stings and which of course determines the quantity of venom pumped into a prey depends on some variables. The first is the size of the spider being stung. The second which could be connected to the first is the resilience of the prey. Larger spiders receive multiple stings and of course large doses of venom, while opposite is the case for the smaller spiders. There seems to be this body-mass index (BMI) factor in determining the dose of venom a spider prey should receive before it becomes paralyzed and not killed. However parasitoidal/predatory efficiency cannot be guaranteed here. The fact that some of the prey die in the process shows that the predatory aggressiveness of the wasp is more at play than determining how much dose of its venom is just sufficient to paralyze and not kill its prey. It is known that the end game is not to kill the prey but paralyze it for the upcoming larva which must not have decaying but fresh food. Consequently, the preys that die in the predator-prey struggle are not flown to the nest but dropped.

As shown in table 1; the number of spiders used in provisioning a cell or nest chamber was not dependent on the carrying capacity of the chamber. There is a positive correlation ($p > 0.05$) in the internal surface areas (ISAs) of the measured nest cells. Rather, it seems safe to say that the sizes and by inference the masses of the prey is a determinant. Take for instances a cell having just three spiders and another having fifteen. It was true that the masses of the spiders in each cells are not the same (see figure 1), but to say as held by Elgar and Jebb (1999) that the female mud-dauber by

instinct determines a cell capacity using the masses of the spiders seem uncertain in this case. Note that the field experiment conducted showed that the wasps ceased their provisioning when they discovered that the cells were filled to capacity after drawing out the second prey. To have sealed up a nest cell without even laying an egg and with only two small spiders (with the last one drown out in a fake full capacity) appeared to send a signal of the wasp leaning on numbers and volumetric capacity rather than masses. It is fascinating however to note that the female mud-dauber responded to disrupted provisioning by being restless at first and then paused before dropping the prey it brought.

5. Conclusion

The Nigerian solitary wasp *Sceliphron servillei* is a rapid flyer. The intrigues contained in its natural life are hardly noticed. Unlike the social hymenoptera such as the bees which use progressive provisioning, it utilizes mass provisioning- a behaviour which contains a whole realm of natural science. It is a prey-specific parasitoid which uses only spiders from the family *Arachnida* for its progeny which it never sees. Perhaps medical science can learn from and exploit its venom in the fields of anesthesia and stasis as it can keep its prey just paralyzed for days without.

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