REVIEW OF THE DEFENSIVE NATURE, MALE TERRITORIAL BEHAVIOR, AND FEMALE HUNTING BEHAVIOR OF THE WASP GENUS, *PEPSIS*, COMMONLY KNOWN AS THE TARANTULA HAWK

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Abstract

The defensive nature, territorial behavior, and host hunting behavior of members of the wasp genus, *Pepsis*, commonly known as tarantula hawks, will be covered in this review. Evidence suggests that these pompilid wasps have some of the best primary and secondary defenses that exist in nature and some researchers have gone as far as stating that they nearly write the manual for insect defenses. It has been observed that some male tarantula hawks will obtain and defend territorial shrubs on desert mountaintops while others will move from site to site, generally fleeing from other males defending their territory. Confrontations between visiting intruders and territorial defenders rarely escalate to a pursuit in a behavior known as an "ascending flight". There can be a vast difference between the sizes of male tarantula hawks and the significance of this variety in sizes and how it relates to territory and mating is the focus of various studies. These studies show that although male body size may not play a direct role in the success for attracting females, it does play a large part in obtaining and defending territory. The behavior of the female tarantula hawk when it is hunting for a host to place its egg in has been the subject of interest in popular and scientific literature since the 1920s. Female wasps use spiders, generally large theraphosid tarantula spiders, as a food source for their

larvae. The female wasp will paralyze the spider by stinging it, then she will drag her victim backward into the spiders nest or a pre-constructed burrow where she will plant an egg on the abdomen of the paralyzed spider. The larvae will feed off the paralyzed spider until it becomes a wasp, slowly killing the spider during the process. Studies have also shown that female tarantula hawks can improve their chances of successfully catching a spider with more experience. The more times they hunt, the more efficient they will become and therefore they can spend more time on foraging and reproduction.

Introduction

Tarantula hawks are large wasps that feed on the nectar of flowering plants but hunt large, theraphosid spiders as host for their predatory larvae. In America and Mexico, there are around 25 known species and subspecies that mainly live in the desert of southern Arizona and northern Mexico. As their name implies, female wasps will actively search for either male or female tarantulas both in the open and in their burrows. Once located, the female will attack the spider, sting and paralyze it, then drag it into its burrow or a pre-constructed burrow nearby before laying an egg on the spider's abdomen. The paralyzed spider will then serve as a food source for the larvae. The female displays elaborate hunting and host-paralyzing reproductive behavior whereas the male exhibits sophisticated territorial defense and patrolling behavior that is closely related to their size and their ability to find and copulate with female wasps. The tarantula hawk has evolved elaborate defensive characteristics including metallic black or blue-black bodies, bright orange wings, and one of the most painful stings in the insect world. The combination of their territorial behavior, their hunting behavior and reproductive characteristics, and their extensive evolved defenses makes the tarantula hawk a fascinating insect to study.

Discussion

Territorial behavior

There can be a considerable difference between the sizes of males within both vertebrates and invertebrate species. Typically in nature, larger males tend to have a competitive advantage when both defending territory and mating with females. Males of the tarantula hawk wasp species *Hemipepsis ustulata* have a considerable variable when it comes to their body weight. Their size can range from 6mg to 56mg meaning that some males are nine-times larger than others.

During the mating season, which occurs in spring months, some male tarantula hawks will perch in and defend, for several hours each morning, small trees and shrubs along ridgelines and hilltops (Alcock & Kemp 2005). While some males defend, other males will cruise from territory to territory generally being chased off by the defending males (Alcock & Bailey 1997). These territories are typically distributed linearly along ridgelines and preference / appeal for the wasps are those plants that sit higher along the ridge than their neighbors. It also appears that the size and appearance of the plant also plays a role in how desirable it may be to a male wasp. Alcock points out in his article, "Territorial Preferences of the Hilltopping Wasp *Hemipepsis ustulata* (Pompilidae) Remain Stable form Year to Year," that this is the case because the climate in the desert where these wasps live causes these plants to change very little from season to season and their conspicuousness remains the same. Therefore, it is not surprising that the same plants each year are deemed the most desirable for the male wasps (Alcock 2008).

Defending / resident males will scan for passing males who may be challenging their territory as well as for females who may be passing by, although the latter occurs very rarely. Resident males are visited by passing males far more often than by females (Alcock & Bailey 1997). However, Alcock and Johnson observed and commented in their article, "Male Behavior in the Tarantula-Hawk Wasp *Pepsis thisbe* Lucas (Hymenoptera: Pompilidae)," that males apparently can discriminate between females that are unreceptive and are only foraging and those that could be potential mates (Alcock & Johnson 1990). If a female does pass by, the male will pursue and grasp the female in flight. The pair will then fall to the ground and briefly copulate before separating. The female typically will leave the area and the males return to their perch (Alcock & Bailey 1997).

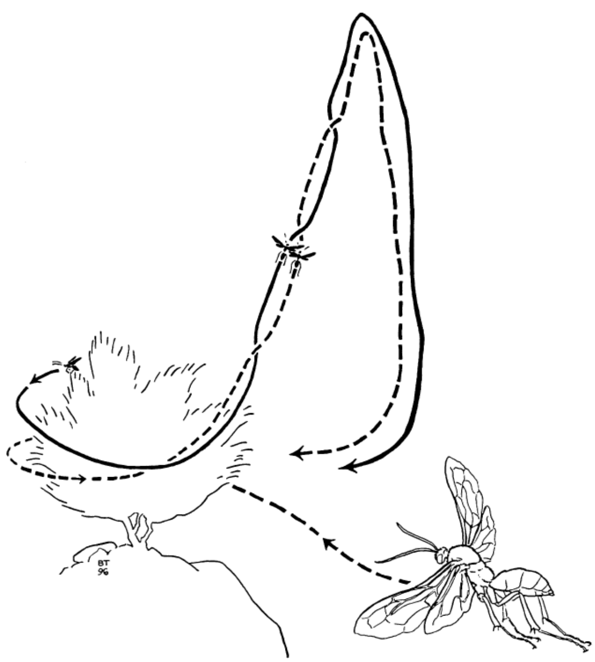

Fig. 1. A diagrammatic representation of an ascending flight between two male tarantula hawks. The solid line represents the resident and the dashed line represents the intruder (Alcock & Bailey 1997).

When these males do leave their perches to fly after other male intruders, typically a brief chase will occur often resulting in the intruder leaving the territory. Rarely, these encounters will result in both males conducting an elaborate vertical spiraling flight until the intruder retreats (Alcock & Kemp 2005). This competitive behavior is known as an "ascending flight (See Fig. 1)". These flights typically last around 20 seconds and can often reach heights of 20 – 50 meters before one wasp dives back to the territory in dispute. In some cases, these competitions can occur multiple times in succession lasting up to an hour. Interestingly, even in competitions that resulted in multiple and lengthy ascending flights, the resident male almost always retained their territory. This behavior lead researchers to conduct studies on why this might be the case. (Alcock & Bailey 1997).

Alcock and Johnson posed a very similar question, why patrol a series of different foraging sites instead of defending a single flowering shrub or tree? Previous studies by Alcock suggest that patrolling, as opposed to defending, will yield more contacts with females when (1) the travel time between the sites is low, (2) there isn't much of a difference in the probability of mates being at one site or another, and (3) the amount of other males that the patroller will encounter from site to site is low (Alcock & Johnson 1990).

Alcock and Kemp also conducted a 25 year study and recorded their observations and research methods in their article, "The Behavioral Significance of Male Body Size in the Tarantula Hawk Wasp *Hemipepsis ustulata* (Hymenoptera: Pompilidae)" in order to answer the above question and to better identify how male body size relates to territorial defense and to mating success. Over those years, they captured both resident and patrolling males in order to measure their size and observe their behavior. They observed that typically, larger males were the territorial holders and smaller males were the patrollers. Out of the 28 matings they observed, 20 of them were by known territory holders and just eight of them were by patrollers. This led them to conclude that larger, territorial males have more success in mating than their smaller, patrolling counterparts. It also prompted them to ask if there was an evolutionary shift toward larger body size over time. Their data was puzzling because over the 25 years they studied these wasps, they saw no major difference in the mean size of the males. They concluded that body size must not be the only attribute that contributes to male success in mating and although increased frequency of alleles is what contributes to the development of larger male wasps and is what leads females to lay male eggs on larger spider prey, both small and large males are mating with females with relatively equal consistency resulting in the continuation of both small and large male wasps (Alcock & Kemp 2005). To further confuse their conclusion on the relation between male mating success and size of the wasps, multiple other studies have shown that the size of the wasp directly relates to the size of the larvae and the size of the larvae depends on the size of the host spider the female wasp successfully hunts (Punzo 2005).

Hunting Behavior

Female Pompilid wasps do not hunt spiders as a source of food. Their food source comes from the nectar of a variety of flowering plants (Punzo 2005). Rather, they hunt the spiders in order to utilize their bodies as a food source for their larvae. When the female wasp spots a tarantula or a tarantula burrow, she will typically approach it and either lure the spider out of the burrow, enter the burrow, or directly engage it on the ground. In all occasions, the wasp will inspect or “groom” the spider in what is known as antennation (Punzo & Garmen 1989). Punzo’s study in his article, “Experience Affects

Hunting Behavior of the Wasp, *Pepsis Mildei* Stål (Hymenoptera: Pompilidae)" has shown that at this point the spider will do one of three things. About 60% of the time, the spider will remain motionless. About 35% of the time, the spider will elevate its abdomen and stilt its legs. Only about 5% of the time will the spider exhibit threat behavior by elevating its body and extruding its fangs. Out of the 32 experiments conducted, not once did a spider attempt to flee or bite the wasp (Punzo 2005). Punzo and Garmen suggest that the passive nature of the tarantula could be attributed to the antennation of the spider somehow inhibiting the aggressive attack nature of the spider. After antennation, the female wasp will approach the spider and a short bout of combat will ensue typically resulting in the spider being stung and paralyzed by the wasp. The paralyzed spider is then dragged into their own burrow or a pre-constructed burrow where the wasp lays an egg on the abdomen of the spider. She then covers up the burrow with dirt, and moves on in search of more prey (Punzo & Garmen 1989).

Punzo and Ludwig explain in their article, "Behavioral Responses of *Pepsis* thisbe (Hymenoptera: Pompilidae) to Chemosensory Cues Associated with Host Spiders," that it was unclear how and why a wasp chooses a spider for a host. They observed that male spiders are usually encountered by female wasps as they wander over the ground in search of food or females. Female spiders are the ones that are often found within or directly outside their burrows. The researchers conducted a series of experiments to answer that question.

They hypothesized that the wasp responded to chemical stimuli given off by the spiders. They collected approximately 300 male and female spiders both from their burrows and from the open ground of two species, *A. moderatum* and *A. texense* with the amount of each species being similar. Both species of spiders were found to inhabit the same area as the tarantula hawk species, *P. thisbe.* They also collected a species of flour beetle, *T. confusum* in order to test how the wasp would respond to the chemical scent of an unknown species. The total amount of wasps collected was around 1000. They collected the chemicals from the spiders and beetle by lining their enclosures with absorbent filter paper for a week prior to testing. They then lined the floor of a rectangular plastic chamber with absorbent paper half with sprayed tap water and half with the paper collected from each of the two spider species and the beetle species. They then placed the wasp in the chamber and observed which part of the chamber it was attracted to. It was clear from the results that the female wasps were much more attracted to the chemical cues of the spider species, *A. moderatum* than the other two (See Fig. 2). Because the two species of spiders are similarly distributed throughout the wasp's natural habitat, the difference in the wasp's preference lends to the fact that they

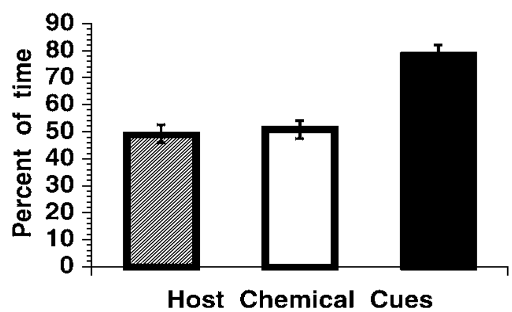

Fig. 2. Mean time (min) spent by female wasps, *Pepsis thisbe* on filter paper containing chemical cues.
Striped bar: Novel Beetle, *Tribolium confusum*.
Unshaded bar: Spider, *Aphonopelma texense*.
Solid bar: Spider *A. moderatum* (Punzo & Ludwig 2005).

are making their decision based on chemical cues rather than host size or availability (Punzo & Ludwig 2005).

Cazier and Mortenson observed and commented in their article, "Bionomical Observation on Tarantula-Hawks and Their Prey," that the majority of female tarantulas are caught and paralyzed by the wasps outside their own burrows (Cazier & Mortenson 1964). They cited several previous studies that debated whether the wasp would actually go into the burrow of the tarantula or not. Some studies showed that the wasp would simply wait outside for the tarantula to appear, while others stated that the wasp would actually go inside the burrow or vibrate some of the webbing at the burrow entrance to entice the tarantula to exit. They conducted several experiments based on these previous studies in order to better understand how the tarantula hawk catches or lures its prey

They first located several silked-over tarantula burrows all within 15m of each other. In one experiment, a wasp was placed in a large open container with a mesh bottom. The container was turned upside down with the open end over one of the silked-over burrows. The container was removed and the wasp immediately went to the burrow, cut her way through the silk covering and entered. Within seconds, the tarantula burst out of the burrow and stood elevated with her legs over the entrance. After a few minutes, the wasp emerged from the burrow as well and flew away without an altercation.

The same procedure was followed on the third experiment. This time however, when the wasp approached the third silk-covered burrow, she vibrated the covering with her wings and within seconds, the tarantula burst through the silk and grabbed the wasp.

It then released her and she flew away, again without any attempt to sting or paralyze the tarantula.

Cazier and Mortenson recognized that their field experiments were limited and that their controlled environment may have been responsible for some of the puzzling behavior they observed. The main one being the reason, or lack thereof, for the wasp not to sting and paralyze the tarantula. One of the reasons, they believed, was because in one of the experiments, the tarantula was rather large and had a much heavier body leading them to hypothesize that the tarantula hawks prefer smaller, more manageable tarantulas. The observations did confirm, however, that the wasp did use several methods to get the tarantula out of its burrow (Cazier & Mortenson 1964). It important to note that it has been observed in research conducted since 1964 that tarantula hawk larvae provided with larger hosts attain larger adult body size (Punzo 2005). That being said, as previously stated, large male size does not necessarily correlate with successful competition for mates (Alcock & Kemp 2005).

No. of encounter	$\bar{X} \pm SD$[1]
1	237 ± 8.41
2	233 ± 5.78
3	196 ± 7.34
4	177 ± 6.85
5	168 ± 3.77
6	167 ± 5.21
7	163 ± 6.34
8	165 ± 2.19

Table 1. Total time (min) required for a female wasp of the species *Pepsis Formosa* to complete the hunting sequence. Values represent testing of 17 wasps (Punzo & Garmen 1989).

Punzo observed in several of his experiments that the female wasp has the ability learn and improve her hunting skills the more time she successfully stings and paralyzes a host spider. He points out that the reduction in time for overall hunting sequence reflects an increase in the decision-making abilities of the wasp (Punzo 2005). More importantly, he adds, decreasing the amount of time required to complete the hunting sequence also minimizes the amount of time a female needs to spend gaining energy to hunt by foraging and thus reducing the amount of time it spends open to attack from predators. (See Table 1) (Punzo & Garmen 1989). This ability to learn and improve its hunting skills and overall fitness contributes to the overall impressive defensive nature of the tarantula hawk.

Defense

Schmidt mentions in his article, "Venom and the Good Life in Tarantula Hawks (Hymenoptera Pompilidae): How to Eat, Not be Eaten, and Live Long," that "Tarantula hawks nearly write the manual for insect defenses." They possess both primary and secondary defense systems. The primary systems include their stinger, the venom it contains, and their hard, close fitting and smooth integument. Their secondary defense systems include their bright colored wings and shiny body, sharp and effective defensive leg spines, the odor they express when they are attacked, as well as other not so common thought of defenses such as long lifespan, the aggregation of the wasps in local areas, and the mimicry by other insects.

Schmidt goes on to mention that it is well know in the biological community that one of the primary defenses of the tarantula hawk, the sting, is extremely painful. To this regard, he mentions the case of researcher Howard Evans who was enthusiastically attempting to reach into a net to retrieve where he had caught around 10 female wasps. He quotes, "Undeterred after the first sting, he continued, receiving several more stings, until the pain was so great he lost all of them and crawled into a ditch and just bawled his eyes out." In contrast to the extreme pain the sting can give, their venom is remarkably non-lethal to mammals. At best, it is only about 5% as lethal as that of a honey bee or yellowjacket wasp, 2% of that of a bullet ant, and 0.2% that of a harvester ant. This significant difference in pain and venom is actually the key to the wasp's ability to both hunt / paralyze its prey and ward off predators. The venom appears to induce pain but no toxicity in vertebrates alone which wards off predators. With their spider hosts, they are still able to sting and paralyze them enough to keep them alive so their larvae can feed.

As previously mentioned, it is Schmidt's opinion that tarantula hawks are among the best defended animals on the planet. He is aware of no examples of active hunting of the wasp, even the relatively harmless males, by common insect predators such as reptiles, amphibians, and mammals. He believes the main reason for this is the power of the wasp's sting. When individual species' have good defenses, natural selection commonly operates in other ways to further enhance that species' survival. This could be one of the possible reasons for the development of the wasp's secondary defenses. The extensive mimicry of other insects, for example, is a direct result of the success of tarantula hawk defenses. The bright and shiny colors of the wasp's body and wings are an obvious sign to predators that the insect is dangerous and because of this, several other insect species have evolved to have similar color patterns. The Mydas fly, or *Myda luteipennis*, while being only a fly, has a black body, bright yellow / orange wings and behaves almost like the tarantula hawk. *Lytta fulvipennis* is a species of blister beetle that also has a black body with yellow / orange wings and resembles the tarantula hawk when moving along the ground. Female tarantula hawks benefit from the mimicry traits of other insects because the more that insects look dangerous, the more predators will avoid them. Male tarantula hawks benefit from mimicking the females and the species' that are doing the mimicking benefit because predators know to avoid their wasp-like colors or behaviors (Schmidt 2004).

Conclusion

Tarantula hawks are capable of a variety of complex insect behavior ranging from male territorial defense, female hunting of host spiders, to primary and secondary defenses. Not only are both large and small males able to defend territory and reproduce, females are able to attack, paralyze and lay an egg host spiders much larger in size. Their extensive defenses have allowed them to live much longer lives than typical insects and they have very little in the way of natural predators. Their complex behavior has fascinated researchers for decades and allowed for extensive experiments to be conducted resulting in elaborate and detailed articles being published.

References

Alcock, John. (2008). "Territorial Preferences of the Hilltopping Wasp *Hemipepsis ustulata* (Pompilidae) Remain Stable form Year to Year." *The Southwest Naturalist.* Volume 53, No. 2. 5p

Alcock, John, Darrell J. Kemp. (2006) "The Behavioral Significance of Male Body Size in the Tarantula Hawk Wasp *Hemipepsis ustulata* (Hymenoptera: Pompilidae)." *Ethology*. Volume 112. 7p

Alcock, John, Michael D. Johnson. (1990). "Male Behavior in the Tarantula-Hawk Wasp *Pepsis thisbe* Lucas (Hymenoptera: Pompilidae)." *Journal of the Kansas Entomological Society.* Volume 63, Issue 3. 5p

Alcock, John, Winston J. Bailey. (1997). "Success in territorial defence by male tarantula hawk wasps *Hemipepsis ustulata:* the role of residency." *Ecological Entomology.* Volume 22. 6p

Cazier, Mont A., Martin A. Mortenson. (1964). "Bionomical Observations on Tarantula-Hawks and Their Prey (Hymenoptera: Pompilidae: *Pepsis*)." *Annals of the Entomological Society of America.* 8p

Punzo, Fred. (2005). "Experience Affects Hunting Behavior of the Wasp, *Pepsis Mildei* Stål." *Journal of the New York Entomological Society.* Volume 113, Issue 3. 7p

Punzo, Fred. (2005). "Studies on the Natural History, Ecology, and Behavior of *Pepsis Cerberus* and *P. Mexicana* (Hymenoptera: Pompilidae) from Big Bend National Park, Texas." *Journal of the New York Entomological Society.* Volume 113, Issue 1. 11p

Punzo, Fred, Brian Garman. (1989). "Effects of Encounter Experience on the Hunting Behavior of the Spider Wasp, Pepsis Formosa (Say) (Hymenoptera: Pompilidae)." *The Southwestern Naturalist.* Volume 34, No. 4. 5p

Punzo, Fred, L. Ludwig. (2005). "Behavioral Responses of *Pepsis thisbe* (Hymenoptera: Pompilidae) to Chemosensory Cues Associated with Host Spiders." *Journal of Insect Behavior*. Volume 18, No. 6. 9p.

Schmidt, Justin O. (2004). "Vemon and the Good Life in Tarantula Hawks (Hymenoptera: Pompilidae): How to Eat, Not be Eaten, and Live Long." *Journal of the Kansas Entomological Society*. Volume 77, Issue 4. 11p