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Maternal Defensive Behavior of *Umbonia ataliba* Treehoppers

Sarah Anvik

Department of Environmental Studies
College of Arts and Sciences
University of Colorado, Boulder

ABSTRACT

A population of *Umbonia ataliba* (Homoptera: Membracidae) located between 1300 and 1500 m in Monteverde, Costa Rica was studied from October to November 2006. The maternal defensive behavior exhibited by these subsocial insects toward nymphs of different developmental stages was experimentally investigated. The purpose of my study was to determine how the defensive behavior changed from eggs to adults and in response to two different predator types. I attached dead wasps to long wooden sticks and then simulated predator approaches toward family groups of eggs, second instar and fourth instar nymphs. I found that the defensive behavior by females guarding nymphs of different ages differed from random in type and frequency. I determined that female parents with second instars were the most aggressive, and that the most common behavior type among all groups proved to be kicking. In regards to the behavior changes exhibited against predator types, females were generally more aggressive when approached with the black wasp, but there was no significant change in the frequency of behaviors.

RESUMEN

Estudie un población de *Umbonia ataliba* (Homoptera: Membracidae) localizada entre de 1300 y 1500 m en Monteverde, Costa Rica de Octubre a Noviembre 2006. Estudie la conducta defensiva maternal en las diferentes etapas de desarrollo de las ninfas. El propósito de mi estudio fue a determinar como la conducta defensiva cambia de huevos a adultos y en respuesta a dos diferentes depredadores. Concreté avispas muertas a palos de madera y simulé el acercamiento del depredador en grupos familiares de la madre con huevos y ninfas a diferentes edades. Encontré que la conducta defensiva de las hembras al proteger las ninfas, difiere de aleatoria en tipo y frecuencia. Determiné que madres con ninfas en segundo estado de desarrollo son las más agresivas, y el tipo de conducta más común entre todos grupos fue patear. Consideró que la conducta exhibida contra los depredadores difirió porque las hembras estaban más agresiva se acercó una avispa negra, pero con el cambio en la conducta no fue significativo.

INTRODUCTION

Females of the genus *Umbonia* are semelparous, with the ability to produce only one brood of young in their lifetime. Different types of maternal behavior make them subsocial insects. According to Tallamy and Wood (1986) subsocial behavior is the most primitive level of social interaction involving parents and offspring. Subsocial behavior of treehoppers, including *Umbonia*, is restricted to maternal care of eggs and nymphs (Chung-Ping et al. 2004). Egg guarding is the most common form and is defined as the female remaining on top of the egg mass for a period of time after oviposition. In this case the body of the female is used as a shield to protect her young from predation and parasitism (Chung-Ping et al. 2004). According to Zink (2003), guarding behaviors are important for the protection and survival of eggs.

In *U. ataliba* siblings are reared together under the care of the mother who embeds 50-100 eggs into the branch tip of the host plant (Mimosaceae) and then tends the offspring throughout development (Masters 2000). The development stages include eggs, nymphs and adults. Egg development is lengthy and usually lasts about 40 days (Masters 1994). Nymph development, in which the young mature from first to fourth instars, lasts approximately 44 days (Masters 1994). The mother will remain with her young until they reach adulthood.

Since the female is semelparous, her investment in the brood is extremely high and thus she exhibits several types of parental care. Tallamy (1983) describes parental care as any parent-offspring interactions that promote the survival, growth, and development of immature insects. Two types of parental care exhibited by females of this species include behaviors that physically protect the young from danger and those that facilitate offspring feeding. Following egg guarding the mother drills a series of slits in a spiral around the branch tip using her ovipositor (Wood 1973). When the nymphs hatch they cluster around the slits, which facilitate access to the plants vascular tissue. The nymphs remain in this aggregation around the plant's host stem with the mother positioned below (Cocroft 1999). The placement of the mother and the nymphs are essential in allowing the mother to provide another type of parental care, physical.

Maternal defensive behavior in *Umbonia* is crucial for the survival of the brood as they are vulnerable to a number of invertebrates and are highly preyed upon. Their most common predators are wasps, and in Monteverde, assassin bugs (Reduvidae) are common as well. In the case of *Umbonia crassicornis* wasps approach family groups from the air and land on or near the aggregation, attempting to remove nymphs through biting and then pulling them from the branch (Cocroft 2002). In order to protect the brood, the female's defenses have become extremely specialized and include behaviors such as kicking, wing fanning and running towards the predators. These actions are often effective in deterring predators and therefore increase the survival of the brood. Visual and chemical stimuli are both important in allowing the mother to sense predators and actively defend her young (Wood 1975). A study by Wood (1973) on *U. crassicornis* showed that when a brood was left without the mother, 100% of them died within ten days. Maternal defense is therefore important for both eggs and developing nymphs.

The purpose of my project was to observe and compare the mother's protective behavior from eggs to adults in *U. ataliba*. As the nymphs age, they occupy more space on the branch, making it increasingly difficult for the mother to defend them. At the

same time, the nymphs become better suited to defend themselves. My hypothesis is that the mother will defend her brood through all developmental stages but that the effectiveness of the behaviors will vary. My prediction is that the frequency of defensive behavior types will differ as the nymphs age.

METHODS AND MATERIALS

Study site

My study was conducted on a fallow pasture at approximately 1500 m in Monteverde, Costa Rica from October to November 2006. Ten years ago, trees of family Mimosaceae (known host) were planted on this land and occupy much of the property. Many of the tree species, such as *Inga punctata* are clumped, with up to four individuals in close proximity of each other, while others are solitary, such as *Zygia palmanum*. Tree species suitable for examination included *Zygia palmanum*, *Inga punctata*, *Inga sierrae* and *Cojoba costaricensis*.

Group location

Umbonia ataliba groups were located on branch tips of Mimosaceae trees and covered with mesh bags. This ensured that the groups would be safe from predation. Groups were monitored for nymph maturation.

Defensive behavior experiment

Mothers with eggs, second instars and fourth instars were tested for defensive behaviors against simulated black and yellow wasps, both known predators. In order to test the maternal defensive behaviors, it was necessary to imitate incoming predators. To accomplish this, I first collected a dozen dead wasps, half of them black and half of them yellow. I then carefully attached each of the wasps to the pointed end of a long wooden sticks using super glue. I always glued the stick to the underside of the abdomen, leaving the wasps unaltered on the top to create a more realistic appearance.

In order to test the female's behavior, certain abiotic factors were necessary including warm temperatures without direct precipitation; these conditions increased the likelihood of the female displaying active responses. A good indicator of a favorable testing day was the presence of active butterflies. As I approached the group with the wasp, I would gently wiggle the stick in order to simulate the appearance of a flying wasp. The group was approached from both the front and the rear, and the wasp was moved up and down the branch. The wasp was brought close enough to the female and the group for direct contact to take place. I tested each group for two minutes; making tallies next to the demonstrated behaviors. In order to give the female a chance to respond, I allowed her to show a behavior at least five times before stopping to record the data. After two minutes had passed, I made final tallies and re-covered the group. In order to minimize infection, I removed any dead leaves or debris from the mesh bag before placing it over the branch, being careful not to disturb the mother or the young.

With each group I ran tests in a similar fashion, noting environmental conditions and predator type before I began. The five types of behavior I tested for were kicking, fanning, running, covering and tilting by nymphs (Table 1). Each family group was tested for these behaviors on two separate occasions, once with the black and once with the

yellow wasp. The order of testing varied; some groups were approached with the black wasp first and others with the yellow.

Statistical Analysis

A 3x6 contingency table was constructed and examined with a Goodness of fit test; used to analyze maternal defensive behavior against two predator types. Running behavior was not included in the analysis because it never occurred more than once for any developmental age and for some groups it never occurred at all. The tilting behavior is mainly a defense of the nymphs and not of the mother, and hence it was analyzed separately. A Goodness of fit test was then used to analyze the frequency of demonstrated maternal behaviors. A Chi-squared test of independence was also run to determine if females are more aggressive overall towards a particular wasp color morph.

RESULTS

Among the four species of the family Mimosaceae examined for this project, individual females were found on *Z. palmanum* and *I. sierrae*, but family groups were only present on *I. punctata*. I studied 33 different females and their families. The difference in observed versus expected values was significant as it differed from random (Goodness of fit test, $\chi^2 = 131.696$, $p < 0.0001$, $df=10$) (Fig.1). This indicates that the frequency of the mother's behavior deviates from random.

Defense of eggs, second instars and fourth instars

For females with eggs, the most common type of behavior was kicking with 97 (yellow) and 106 (black) occurrences, followed by fanning (4 and 3 respectively). Mothers with eggs more often than expected by random, whereas the frequency of fanning is lower than expected by random (Figure 2)

Next, mothers with second instar nymphs also favored kicking, exhibiting this behavior 134 (yellow) and 154 (black) times. However, the expected value for kicking was less than actually observed. By contrast, mothers with second instars fanned and covered more than expected, showing more occurrences of covering (43 and 56) than fanning (26 and 36) (Fig.2).

Finally, mothers with fourth instar nymphs also demonstrated kicking more than any other defensive behavior, demonstrating it 98 times with the yellow and 121 times with the black wasp. Covering was rare for mothers with this age, who showed this type of behavior only once for both predator types. Similarly, the mothers did not choose to fan very often, although the numbers are significantly higher for fanning than expected by chance (Fig. 1). Also interesting to note is the high number of tilting behavior examined by the nymphs of this age (Table 2). Although tilting is a behavior of the nymphs rather than adults, I compared its frequencies and found that it too differed in frequency from one developmental stage to the next.

Defensive behavior

The defensive behavior most common among all group ages was kicking (Fig. 3). Kicking behavior occurred at the highest frequency with second instar groups, followed by mothers with fourth instars and lastly individuals with eggs. Covering was the next

most common behavior and was only used with seconds, followed by fanning, also used mainly for seconds (Fig. 3). These examinations allowed for the conclusion that mothers with second instar nymphs are the most aggressive of all mothers tested. The total number of defensive behaviors exhibited by the mothers for eggs, second instars and fourth instars were 212, 449, and 256 respectively.

Responses to Black versus Yellow Wasp

Females respond to black and yellow wasps with the same frequency of defense behaviors. However, the Chi-squared test of independence revealed that mothers are overall more aggressive toward black wasps than they are toward yellow wasps showing significance at the .05 level ($\chi^2=8.27$, $df=1$) (Figure 4).

DISCUSSION

My hypothesis for this study was that the mother would defend her brood through all developmental stages but that the effectiveness of different defense behaviors would vary. Thus my prediction was that the frequency of defensive behavior types would differ as the nymphs aged. My prediction was confirmed in this experiment, thus supporting my hypothesis. As predicted, female parents guarded their brood through all stages of development. This is explained by the fact that the mother is semelparous and the survival of the young depends on her. In treehopper species that lay only one clutch, the cost of remaining with the brood are expected to be so minimal that the female should always display extended care (Zink 2003). I also found that the mothers' behaviors varied throughout nymphal developmental stages because some behaviors were more effective than others in deterring predators. For example, covering is not as effective of a behavior for fourth instars as it is for seconds because the nymphs at this age are too large, making it difficult and time consuming for the mother to carry out this behavior. Although the frequency of different behaviors changed with the age of the nymphs, kicking was the most common behavior overall.

In this study, I found that females with eggs showed the least amount of response and movement when approached by a predator. In the case of *U. crassicornis*, Wood (1983) believes that lack of movement enhances cryptic coloration and reduces the vulnerability of parent females while guarding eggs. The main behavior exhibited by mothers with eggs proved to be kicking, with some fanning. The frequency of behaviors shown in this age group is likely due to their position on the branch.

In the later stage, mothers with second instars proved to be very aggressive. They favored kicking over other behaviors followed by covering and then fanning. Mothers with second instars were the only groups to exhibit covering behavior multiple times during a single test. This change in frequency can be attributed to the effectiveness of behaviors used. Although kicking is the most effective when the predator is nearby, when the predator is not within reach, other behaviors must be used. Due to the size and vulnerability of nymphs at this age, covering appears to be a quite effective and easily accomplished way of protecting the brood from predator invasion.

The final groups, fourth instars are unique in that they too act to defend themselves against predators, mostly by tilting. However, when looking solely at maternal defensive behavior, I found that as with other groups, mothers chose to kick

more than anything else. The next highest frequency of behavior observed was fanning. This can be explained using a study on *U. crassicornis*, which found direct movement to be the most effective, followed by fanning, which provides defense without movement toward the predator (Wood 1974). Based on this evidence, it can be concluded that mothers show varied defensive behaviors to be effective at deterring predators.

My study is unique in that it is the first to compare behavior between developmental stages in *Umbonia*. Similarly, it is the first to test for different responses toward predators of different types. Although significant results were not found for a change in frequency of behavior between predators, the females prove to be more aggressive toward the black wasp; although it is unknown exactly why. Some types of black wasps in Monteverde are known to be parasites, though the ones used in the study are not. It is possible that the females act more aggressively because they perceive these wasps as being parasitic; however, this proposal is extremely difficult to prove. In future studies, it would be interesting to include reduvid bugs as predators. Unlike wasps, which approach from the air, these insects approach the group by walking toward them on the branch. Also, if time allowed, it would be helpful to track the same groups throughout developmental stages to see how behavior changed for that specific female. These kind of data would allow for a more detailed analysis, although similar results would likely be obtained.

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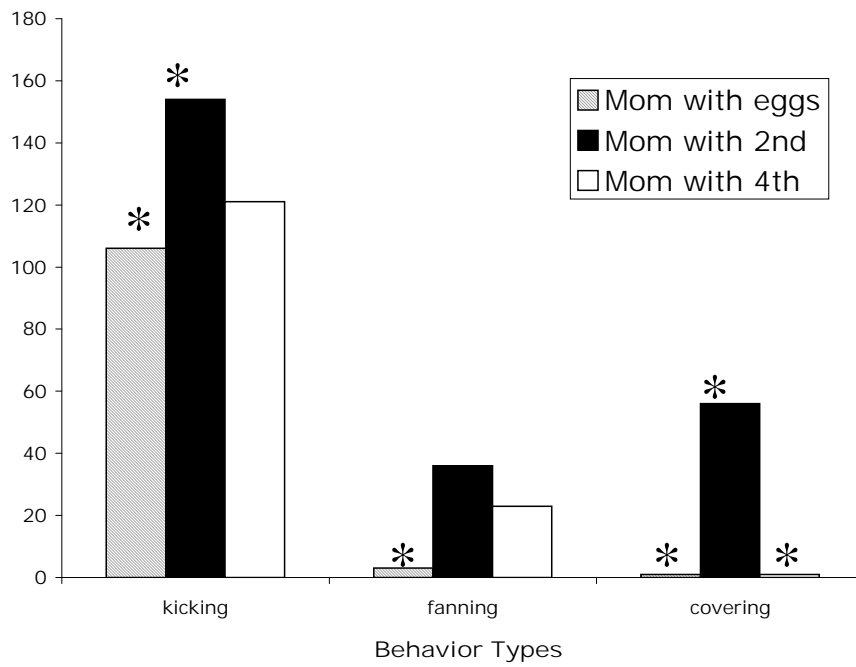
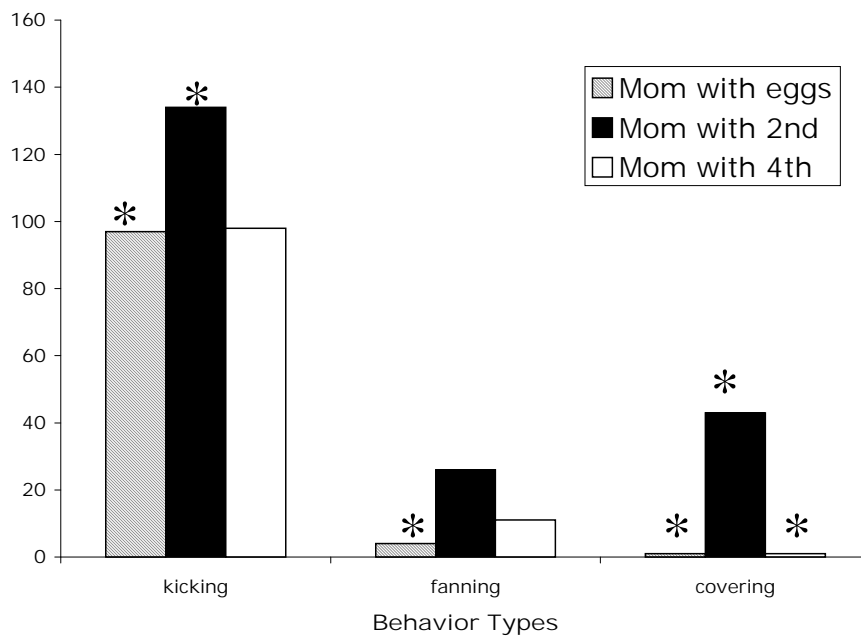
A**B**

Figure 1: The frequency of defensive behaviors (kicking, fanning and covering) exhibited by the mother in response to the black wasp (A) and the yellow wasp (B) across three developmental stages. Asterisks indicate an observed behavior which deviated from random

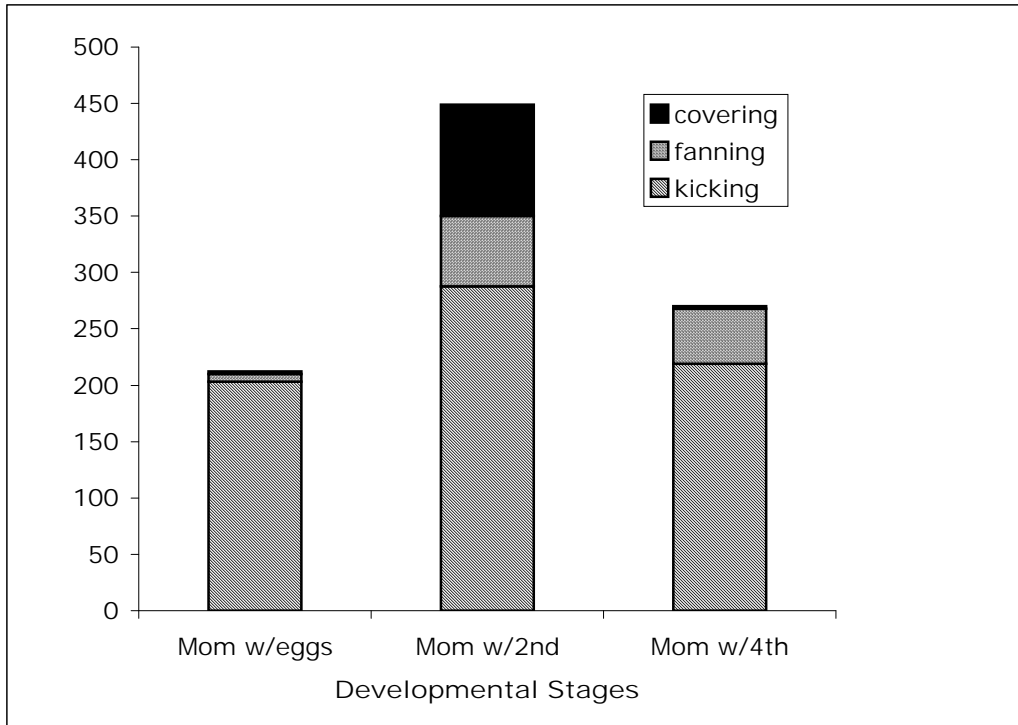


Figure 2: The frequency of behavioral occurrences between developmental stages. This graph demonstrates the aggressiveness of mothers with second instar nymphs compared to other developmental age groups.

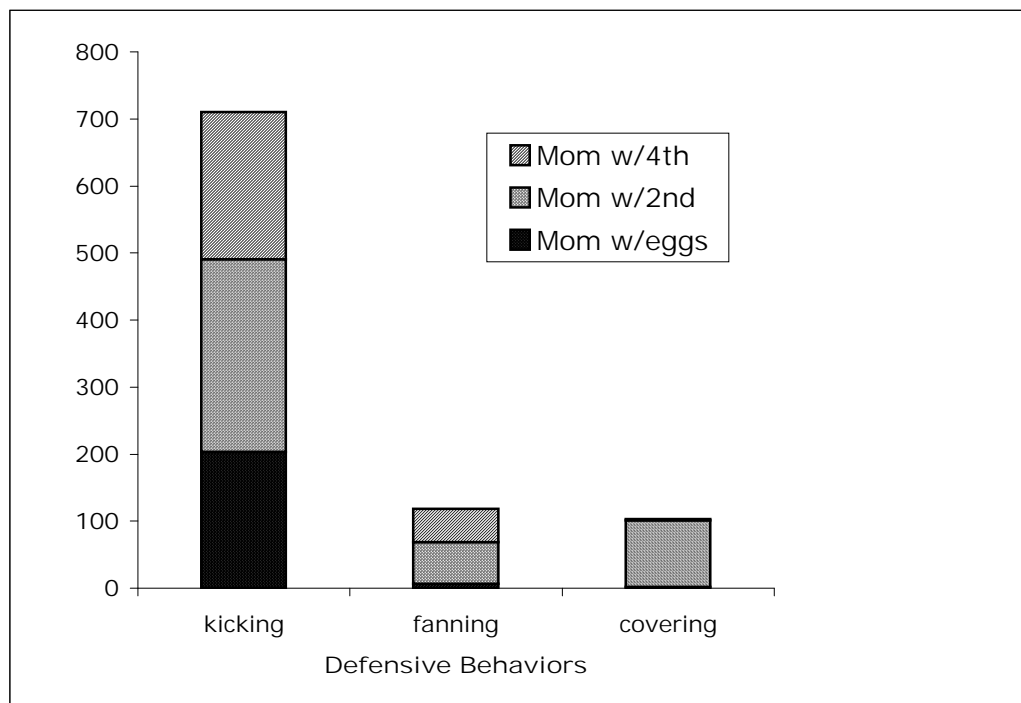


Figure 3: The frequency of observed behaviors occurring across developmental stages. This graph demonstrates that the most common observed behavior is kicking

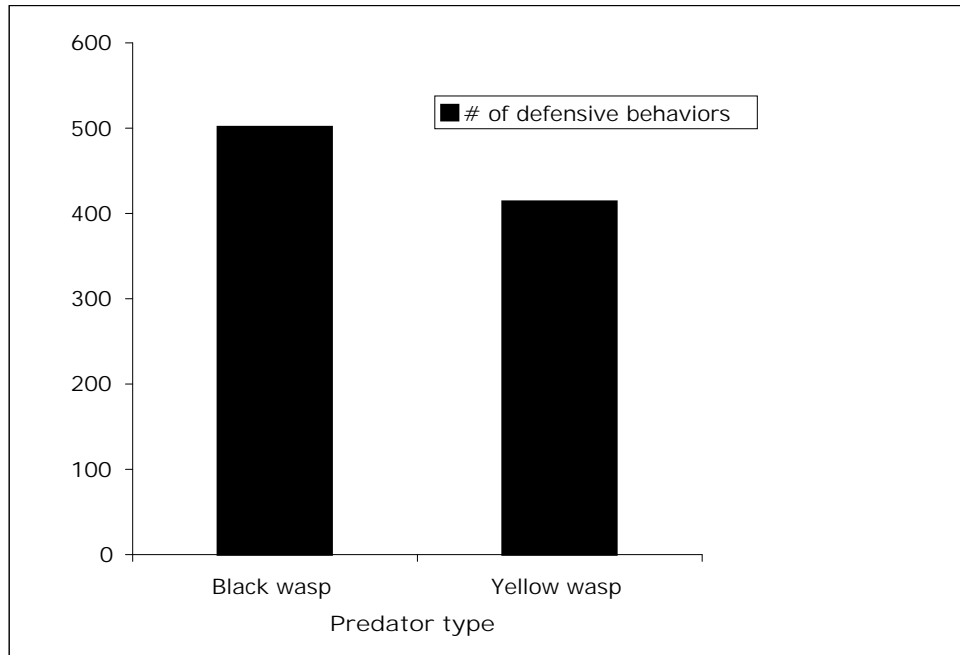


Figure 4: The total number of observed maternal defensive behaviors exhibited in response to black and yellow wasps. Females showed more aggressive behaviors toward the black wasps than the yellow wasps.

Table 1: Descriptions of defensive behavior types

Behavior	Description
Kicking	Took place when the mother was close enough to the predator to touch the wasp with one of her hind legs
Fanning	Took place at various proximities, consisted of mother aggressively fluttering her wings
Running	Took place when the wasp was to on the opposite side of mother, and she quickly move from the terminal end of the branch toward it
Covering	Took place when predator was out of range for physical contact, consisted of her inching along the branch, positioning herself on top of the nymphs
Tilting	Took place when nymphs attempted to defend themselves by lifting their abdomens in a synchronized wave

Table 2: Tilting behavior examined over three developmental stages with two predator types (Yellow and Black wasps).

	Eggs	Seconds	Fourths	Eggs	Seconds	Fourths
	Black	Black	Black	Yellow	Yellow	Yellow
Tilting	0	2	58	0	4	62