Analysis of Stingless Bee Aggression

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(*T. spinipes* forager attacking *M. rufiventris* forager at a food source)

I. Principles introduced in this exercise

- **A. Aggression: how they attack**
- **B. Defender's perspective: what to attack**
- **C. Results of aggression**

II. Introduction

The social regulation of aggression plays an important role in competitive interactions among animals (Moynihan 1998); the structure of arthropod communities (Reitz and Trumble 2002); invasion ecology (Holway et al. 2002); and the evolution of animal behavior (Maynard-Smith and Harper 1988). However, questions remain concerning the detailed effects of group size on *individual* aggression during aggressive encounters between groups (Archer 1988), even in primates (Bernstein and Ehardt 1985; Camperio 1986; Goodall 1990; Stanford et al. 1994; Gros-Louis et al. 2003).

In social insects, group aggression plays a vital role in ants, social bees, and social wasps during nest defense and, in some species, during foraging (Wilson 1971; Michener 1974; Breed et al. 1990; Hölldobler and Wilson 1990). For example, Wilson (1971) reported that individual *Ancanthomyops claviger* ants increased their sensitivity to alarm odors when in larger groups. Interspecific competition over limited food sources has led to the evolution of aggressive group recruitment systems in stingless bees (Hymenoptera, Apidae, Meliponini), one of the most important native Neotropical pollinators (Johnson and Hubbell 1974; Johnson and Hubbell 1987; Roubik 1989; Nagamitsu and Inoue 1997; Slaa et al. 1997; Kevan and Imperatriz-Fonseca 2002; Slaa 2003; Nieh et al. 2004). Such aggressive competition may be costly and critical to colony survival, especially during periods of relative food dearth (Roubik 1982; Roubik 1989). Johnson & Hubbell (1974) recorded 63% mortality (1812 dead bees) after a two-day battle between three colonies of *T. corvina* (Lepeletier 1835) over sucrose solution baits.

However, relatively little is known about the detailed patterns of aggressive behavior (Johnson 1974) that constitute meliponine dominance styles, or the strategies and behaviors that individuals or groups typically employ to attain dominance (Cooper and Bernstein 2002). This exercise focuses on defining behaviors involved in aggressive encounters between bee species in order to better understand these interactions.

III. Materials & Methods

We are going to look at several movies which show bees battling over a food source: a sugar solution feeder (pink platform) or a flower. The *T. spinipes* foragers are the smaller, more numerous black bees and the victim is a species of *Melipona*, in these videos the larger furry bee. Unlike honeybees, stingless bees do not have stingers so they fight with their jaws (mandibles).

T. spinipes vs. *M. subnitida* 1
[Quicktime Movie]

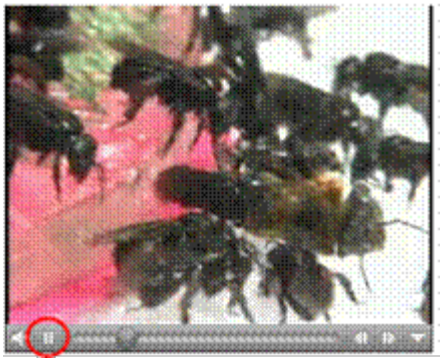
T. hyalinata vs. *M. rufiventris*
[Quicktime Movie]

T. spinipes vs. *M. subnitida* 2
[Quicktime Movie]

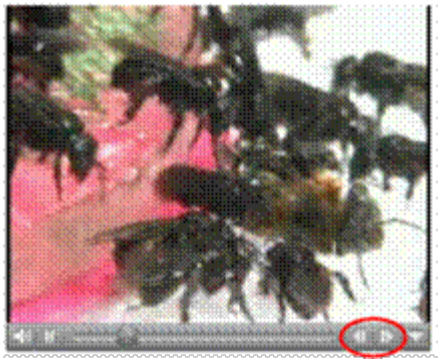
T. spinipes vs. honeybee
[Quicktime Movie]

T. spinipes vs. *M. subnitida* 3
[Quicktime Movie]

A. Click on the link titled "*T. hyalinata* vs. *M. rufiventris*" to open the Quicktime movie. Once the file has opened and begins to play, count the number of bees attacking the victim. If the bees are moving too fast, first watch the video in real time, and then watch it frame-by-frame.



1. Click on the pause button



2. Click on the forward or back button

The Aggressor

B. *Choose one of the black bees (*T. spinipes*) and determine her attack intensity throughout the video. Define the attack intensity using the following table.

Level I: low intensity threats (facing opponent and wide wingspread) without direct contact
Level II: brief body contact (for example, a quick bite)
Level III: extended biting and pulling
Level IV: wrestling (individuals are locked together by leg gripping and/or mandible contact)
Escape: attempting to walk or fly away while being restricted from moving away by attackers
*Definitions based on Johnson & Hubbell (1974), and Nieh et al. (2005).

Here is an example of a sample table you could draw up. Each student can fill in a different column of the table.

Sample Table 1: Aggression classifications from *T. hyalinata* vs. *M. rufiventris*

Subject Bee	Attacker 1	Attacker 2	Attacker 3	Attackee 1
Level of Aggression	Level III	Level IV	Level II	Escape
Target Region	abdomen & thorax	head	abdomen & thorax	none

C. Does the attack intensity of your bee change? Does it increase or decrease? If it does change, then make a new table showing that change at two different points in time. For example, create a "beginning" table and an "end" table.

Sample Table 2: Aggression classifications from *T. hyalinata* vs. *M. rufiventris*
BEGINNING

Subject Bee	Attacker 1	Attacker 2	Attacker 3	Attackee 1
Level of Aggression	Level III	Level IV	Level II	Escape
Target Region	abdomen & thorax	head	abdomen & thorax	None

Sample Table 3: Aggression classifications from *T. hyalinata* vs. *M. rufiventris*
END

Subject Bee	Attacker 1	Attacker 2	Attacker 3	Attackee 1
Level of Aggression	Level II	Level III	Level II	Escape
Target Region	head	head	abdomen & thorax	none

The Victim

D. Define the region of the body being targeted by each attacker as either "head" or "thorax and abdomen".

E. Repeat steps **A** though **D** for the remaining Quicktime movies.

The Attack Strategy

Stingless bees, like honeybees, have certain attack preferences. Stingless bees like to attack hairy objects and dark objects. If you think about this, you will realize that bees are drawn towards attacking sensitive areas around the head of a predator. When they attack each other stingless bees can try to cut off wings, legs, or even the head. In fact, you can sometimes see bees flying around with their legs "decorated" with the severed heads of unsuccessful attackers. This happens during group attacks when members of the colony defend the bee being attacked.

F. Can you describe what kind of attack strategy you saw in each of the three videos?

G. How did the victim respond? Since there was only a single victim and several attackers, what would be the best strategy for the victim?

H. If the victim is trying to escape and the attackers want to prevent this, are there any strategies that the attackers should use?

IV. Sample Results

In the *T. hyalinata* vs. *M. rufiventris* video we observed:

*Note the positions of the play bar which tell you where the aggression occurred in the video

Level I aggression

(A *T. hyalinata* forager spreads its wings while moving towards the *M. rufiventris* victim)

Level II aggression

(A *T. hyalinata* forager executes a quick bite as the *M. rufiventris* forager tries to run away)

Level III aggression
(A *T. hyalinata* forager remains on *M. rufiventris* while biting for several seconds)

Level IV aggression
(A *T. hyalinata* forager and *M. rufiventris* victim wrestle with locked mandibles for an extended period of time)

Escape
(*M. rufiventris* attempts to run away while several *T. hyalinata* foragers follow behind)

V. Sample Discussion Questions

A. How did the bees attack?
They exhibited multiple levels of attack intensity from I-IV, threatening, biting and pulling, and locking mandibles for extended periods. In all cases many smaller bees attacked one larger bee.
B. Was there anything in particular that attackers focused on?
The attackers seemed to focus on sensitive areas, such as the head and abdomen.
C. Why might some body parts be attacked over others?
Sensitive areas might be attacked to disable an opponent, for example to keep them from escaping or to keep them from attacking back.
D. What were the results of the aggression? Did the attacker run away?

In most cases the "victim" bee attempted to escape and was held back or pursued by the attacking bees.

E. What does it mean to have a higher level of aggression?

It means that the chances of being seriously injured or killed increase. Thus being aggressive must have some kind of payoff in order to be favorable in terms of the aggressor's survival and reproduction.

F. What kinds of animals do you think this kind of attack would be effective on?

The biting attacks of stingless bees would probably only be effective on other small insects, because their mandibles are not large enough to bite anything substantially larger in size.

G. Have you ever seen a bee attack before or been attacked?

You could talk about your personal experience, or that of someone you know.

H. How do you think the bees evolved their particular strategy of attacks?

Bees that were intensely competing for foraging sites may have found an advantage to being aggressive. Driving off competitors would allow the aggressive bees to gain access to more food resources and thus increase the survival and reproduction of their colony.

VI. Sample Conclusions

A group of *T. spinipes* bees (attackers) dominated a single larger *Melipona sp*. bee (attackee) in each movie. It appears that the use of aggression by the *T. spinipes* bees in larger numbers may be an effective strategy for warding off the larger *Melipona sp*. bees. It is possible that this aggression strategy could have evolved because attacking in groups allowed the smaller bees to win more "battles" and therefore gain access to more food resources. It is also possible that attacking in groups decreases the chances of injury for the smaller bees, as escalated aggression levels are more likely to lead to serious injury. The attackers did not seem to focus on any one part of the body more often than the other, but there was almost always more than one bee attacking at any one time.

Click here for a worksheet with blank tables and questions

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