

# A comparative analysis of rapid antennation behavior in four species of *Odontomachus* trap-jaw ants

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**Abstract** The exchange of rapid antennal strikes between individuals is a behavior exhibited by many social hymenopterans, largely in dominance contexts within the nest and in aggressive contexts towards non-nestmates. Despite being widely reported, the behavior itself has not been well described or compared between species for the majority of social insect groups. We first document how often rapid antennation is used as an aggressive response to non-nestmates for four species of *Odontomachus* ants. We then use high-speed videography to measure the rate of rapid antennation behavior for these species. We find that rates are neither conserved nor species-specific and average between 19.5 and 41.5 strikes/s. Next, with *O. brunneus*, we compare this behavior as it is performed between nestmates and non-nestmates. We find no context-specific differences in rate, bout length, or number of strikes. We conclude by discussing the evolution of this behavior and its potential utility as a model for understanding aggressive behaviors both inside and outside of the nest.

**Keywords** Antennal dueling · Antennal boxing · Antennal drumming · Dominance · Aggression

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## Introduction

Rapid antennation (abbreviated below as RA; referred to by others as: antennal strikes, antennal dueling, antennal boxing, or antennal drumming) is a behavior commonly observed within many social insect colonies. This behavior is most often reported as antennal strikes exchanged between nestmates in conflict over reproduction or in the process of establishing or maintaining dominance hierarchies (Heinze et al. 1994; Ratnieks et al. 2006). Though often mentioned, RA behavior has rarely been either quantitatively described or compared between species. For ants, measurements of the rate at which these antennal strikes are performed have yet to be made.

Rapid antennal movements directed towards nestmates have been best studied in *Polistes* wasps. While feeding larvae, workers rapidly drum on the cell wall with their antennae (Suryanarayanan and Jeanne 2008). The rates of these antennal movements have been measured in five species and range from an average of 29 to 37.8 strokes/s (Pratte and Jeanne 1984). *Polistes fuscatus*, which has an antennal drumming rate ranging from 25 to 32 strokes/s, differentially feed and drum larvae to influence fat stores and storage protein levels, directing larval development onto a worker or gyne trajectory (Suryanarayanan et al. 2011a, b). Experimental evidence with this species showed that simulated antennal drumming vibrational signals at a biologically relevant frequency (17 Hz), as opposed to random frequencies, influences development, producing adults with reduced, worker-like fat stores (Suryanarayanan et al. 2011b). Antennal drumming in the case of *P. fuscatus* is the most well described example of worker-generated vibrational signals acting as a mechanical stressor affecting the development and physiology of nestmates. Similar vibrational behaviors, though many not involving rapid

antennal movements (e.g. gaster drumming, body vibrations), are seen throughout wasps and other social insects (Hunt and Richard 2013; Jeanne 2009; Jeanne and Suryanarayanan 2011).

Food exchange between social insect nestmates often involve mutual, head-to-head antennal exchanges. In the honeybee *Apis mellifera*, for example, foragers returning to the hive to transfer food to hive-workers exchange RA bouts at an average rate of 13 strokes/s (Goyret and Farina 2003), and food exchange, trophallaxis, between young and hive workers involves rapid antennal exchanges (Montagner and Pain 1971). Trophallaxis in ants can involve similar antennal exchanges (Bonavita-Cougourdan 1984), however, measured rates of these and antennal movements are well below reported rates of RA behavior reported in other behavior contexts (3–6 strokes/s; Lenoir 1982).

In ants, RA behavior has been reported for intra-specific interactions in many species. For example, the following species have all been reported to use RA to establish reproductive hierarchies within the nest: gamergate workers of two *Gnamptogenys* species (Gobin et al. 2001; Lommel et al. 2010), *Harpegnathos saltator* (Penick et al. 2014), *Dinoponera quadricaps* (Monnin and Peeters 1999), *Streblognathus peetersi* (Cuvillier-Hot et al. 2004); queens and workers of multiple *Leptothorax* and *Temnothorax* species (Heinze et al. 1994, 1997; Stroeymeyt et al. 2007); workers of *Neoponera apicalis* (Oliveira and Hölldobler 1990); dulotic workers of *Temnothorax americanus* (Franks and Scovell 1983). However, we are not aware of any quantitative descriptions of RA behavior, such as an estimate RA rate or duration, for ants.

In addition to agonistic interactions within the nest, RA has been observed as an aggressive response to non-nestmates in several species. For example, *Pseudoneoponera tridentata* workers and queens use RA within the colony in establishing reproductive hierarchies and also when acting aggressive towards non-nestmates (Sommer et al. 1994). RA is used as an aggressive response to non-nestmates by fire ants (*Solenopsis invicta*) (Balas and Adams 1996). Queens in oligogynous colonies of the Australian meat ant (*Iridomyrmex purpureus*) rapidly antennate each other in establishing a reproductive hierarchy, while workers outside the nest exhibit similar RA behaviors in territorial interactions with conspecific non-nestmates (Ettershank and Ettershank 1982; Hölldobler and Carlin 1985).

In *Odontomachus* trap-jaw ants, RA has been documented in many contexts. Within the nest, RA has been observed between workers to stimulate foraging in *O. bauri* and food exchange in *O. troglodytes* (Oliveira and Hölldobler 1989; Lachaud and Dejean 1991). *Odontomachus brunneus* workers use the behavior as a means of establishing and maintaining a division of labor, where nest

workers display their dominance to peripheral workers and rapidly antennate them out of nest into the role of a forager (Powell and Tschinkel 1999). They also use RA when policing reproductive workers (Smith et al. 2012) and outside of the nest when being aggressive to non-nestmates (Smith et al. 2013). Queenless *O. simillimus* workers with developed ovaries often perform and receive RA behavior among their nestmates (van Walsum et al. 1998). Finally, in the polygynous species *O. chelifera*, RA between queens is used to form a reproductive dominance hierarchy in the nest (Medeiros et al. 1992).

Through a series of observational experiments, we quantify, describe, and compare RA behavior between ant species and across behavioral contexts. We first document the frequency at which RA is used as an aggressive response towards conspecific non-nestmates in four *Odontomachus* species: *O. brunneus*, *O. rixosus*, *O. ruginodis*, and *O. haematodus*. We then use high-speed video to quantify the rate of rapid antennation for these species. Next, with *O. brunneus* we compare the RA rate, bout duration, and overall number of antennal strikes in potential aggressive (towards conspecific non-nestmates) and dominance (towards nestmates) contexts.

## Methods

### General data collection

*Odontomachus brunneus* and *O. ruginodis* colonies were collected from the MacArthur Agro-ecology Research Center in Lake Placid, Florida. *Odontomachus haematodus* colonies were collected in March 2014 from the Weeks Bay Preserve in Fairhope, Alabama. *Odontomachus rixosus* colonies were collected from the Cardamom Mountains, in the Pursat Province of Cambodia. All ants were housed in Petri dishes nests with moist plaster-lined bottoms. Colonies received a constant supply of water and 20 % sugar water solution and were fed twice a week on live termites and freeze-killed crickets. All colonies were kept under an average temperature of 27 °C. All colonies used in this study were collected as mature queen-right colonies. *Odontomachus brunneus*, *O. ruginodis*, and *O. haematodus* colonies were monogynous with a similarity in number of workers (~200–500). *Odontomachus rixosus* colonies were polygynous and smaller (~50–200 workers).

Behavioral observations were made by placing ants in a clean glass petri dish (5.5 cm diameter) over which a conventional or high-speed video camera recorded a top-down view of the arena. High-speed video was recorded with a FASTCAM 1280 PCI (Photron USA, Inc.) at 250 fps. Upon visual observation of the behaviors of interest a post-trigger

was engaged that recorded the last 3.14 s of footage. Videos were analyzed frame-by-frame. Antennal strike frequency was determined by calculating the number of frames required for the completion of a single antennal strike, per antenna. For the purpose of data recording, the length of a complete strike for a single antenna was defined as the number of frames between when the antenna changes directions away from the recipient of the strike. Only periods with consecutive strikes with an antenna were analyzed; recorded periods of non-rapid antennal movements were not used. Rapid antennal movements were distinguished from other antennal movements by being fast enough to induce blurring in at least one frame during the forward motion of the strike. All statistical comparisons were made in STATISTICA v. 7 software (StatSoft, USA). For all analyses, sample sizes are the number of individuals listed in the description of the experiments below.

### Comparison of aggressive RA usage and rate between *Odontomachus* species

For all four species, we compared how often rapid antennation behaviors are used towards non-nestmates by placing two non-nestmates from the same population (from colonies collected within approximately 1 km of one another) in the observation arena and recording the outcome of the interaction. Video was recorded with a standard speed (30 frames per second) video camera. Workers were left in the arena for a 2-min trial unless rapid antennation was performed before the 2-min mark or aggression between the workers escalated to biting and stinging, at which point the trial was ended. Twenty-five unique pairings of workers were analyzed per species. Workers were drawn at random from the following number of colonies per species; *O. brunneus*: 8, *O. rixosus*: 5, *O. ruginodis*: 7, *O. haematodus*: 9. We compared the frequency at which these behaviors were observed per species by Chi-squared tests.

For the same species we also measured the rate of rapid antennation by placing two non-nestmates from the same population in the observation arena and making high-speed video recordings. We measured average rates for 21 *O. brunneus* individuals (11 bouts, or continuous RA exchanges, with workers from 10 colonies), 8 *O. rixosus* individuals (6 bouts with workers from 5 colonies), 15 *O. ruginodis* individuals (11 bouts with workers from 7 colonies), and 9 *O. haematodus* individuals (8 bouts with workers from 5 colonies). We counted the number of frames between strikes, from start to finish from both antennae, from each bout which resulted in collecting an average of 63 antennal strikes per ant per bout for *brunneus*, 30 for *rixosus*, 42 for *ruginodis*, and 47 for *haematodus*. We compared

species rates by a one-way ANOVA followed by post hoc tests between groups, after confirming normality and equal variance by Levene's test ( $p = 0.41$ ).

### RA bout duration and speed towards nestmates and non-nestmates

For *O. brunneus* we compared RA behavior in aggressive (non-nestmate) and dominance (nestmate) contexts. For nestmate pairings, a worker from the foraging arena was paired with a worker taken from inside the nest. This methodology was used based on the Powell and Tschinkel (1999) report that when *O. brunneus* workers from different parts of the nest interact, dominance behaviors between them are quickly observed. Nestmate data were compared to the non-nestmate data collected as described above.

For *O. brunneus* nestmate we data recorded and analyzed 16 individuals (13 bouts with workers from 6 colonies). Only continuous rapid antennation events were considered.

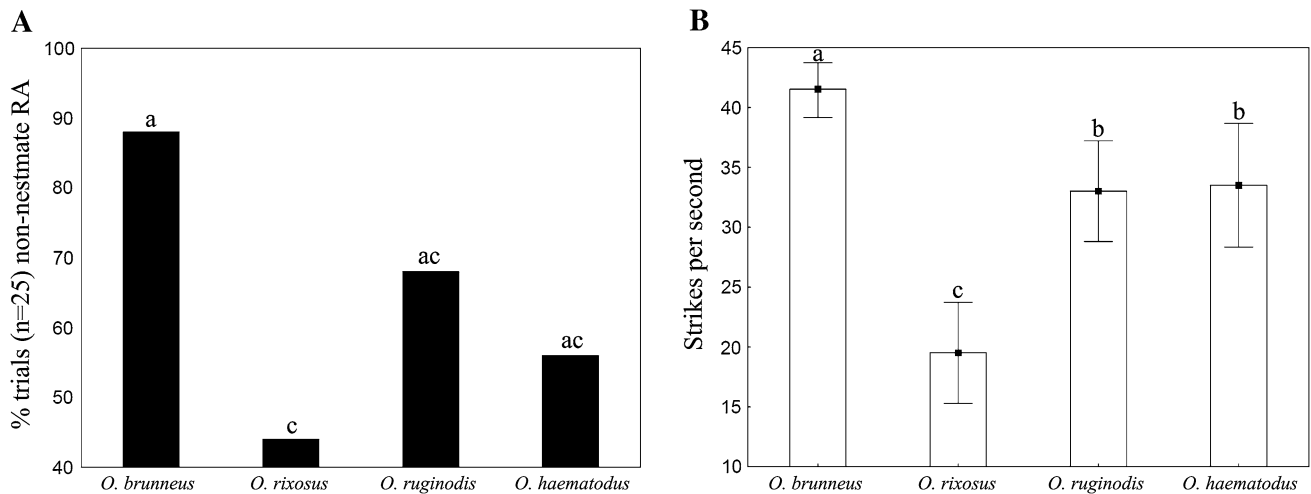
For all individuals we measured three things: the average RA rate of strikes per second for the bout (measured as described above), the duration of the bout, and the total number of rapid antennal strikes performed. These data were compared between nestmate and conspecific non-nestmate bouts. All statistical comparisons were Student's *t* tests (2-sided *p* values are reported) when the normality of the data was confirmed and equal variance of the groups was confirmed with Levene's test  $p > 0.05$ .

## Results

In all four species, 100 % of all the recorded rapid antennation bouts were face-to-face interactions where the ants were in constant antennal contact with each other. 87 % of all recorded rapid antennation bouts were mutual and simultaneous exchanges, in the remaining bouts only one ant performed the behavior.

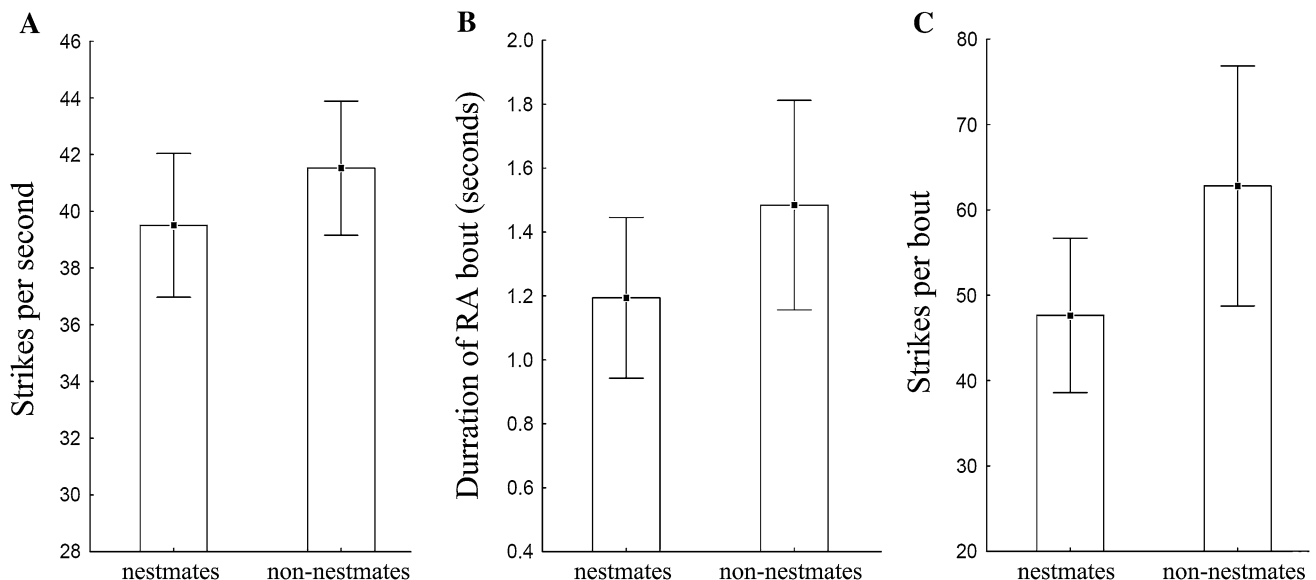
### Comparison of aggressive RA usage and rate between *Odontomachus* species

Rapid antennation was performed in an aggressive context, between non-nestmates, by all of the *Odontomachus* species we studied. *O. brunneus* performed RA towards non-nestmates in 88 % of our trials which was statistically more often than *O. rixosus* and similar to *O. ruginodis* and *O. haematodus* (Fig. 1a). *O. brunneus* strikes are the most rapid, averaging 41.5 strikes/s which is significantly faster than all other species (Fig. 1b). *O. rixosus* strikes (average



**Fig. 1** A comparison across *Odontomachus* species of how often (a) rapid antenation is used in aggressive, conspecific non-nestmate interactions and the rate of rapid antennal strikes (b). a Chi-square test across all species  $\chi^2(3, N = 100) = 11.45, p < 0.01$ , letters denote

pairwise statistical differences according to Holm–Bonferroni corrected  $p$  values. b Means and 95 % confidence intervals; ANOVA  $F(3, 49) = 24.88, p < 0.001$ , letters indicate significant differences between groups ( $p < 0.05$ ) based on Tukey's HSD post hoc tests



**Fig. 2** A comparison of strikes per second a and bout duration b and the number of strikes per bout c of RA behavior between nestmates and non-nestmates of *O. brunneus*. Means and 95 % confidence intervals;  $t > -1.69, p > 0.06$ , all comparisons

19.5 strikes/s) are the slowest, while the rates of both *O. ruginodis* and *O. haematodus* are not statistically different (average 33, and 33.5 strikes/s; Fig. 1b).

#### RA bout duration and speed towards nestmates and non-nestmates

Rapid antenation behavior of *O. brunneus* is not statistically different when performed between nestmates and non-nestmates in strikes per second (Fig. 2a), duration of bout (Fig. 2b), and strikes per bout (Fig. 2c).

#### Discussion

Antennal strike frequencies were neither conserved across our study species, nor specific to individual species. The ranges of average RA rates (19.5–41.5 strikes/s) found in four *Odontomachus* species is larger than the average antennal drumming rates reported across five species of *Polistes* wasps (29–37.8 strokes/s; Pratte and Jeanne 1984). Exceptionally fast antennal movements in the genus *Odontomachus* also occur when these ants retract their antennae immediately before releasing their extremely fast

predatory mandible snaps (Ehmer and Gronenberg 1997). Ehmer and Gronenberg (1997) reported that *Odontomachus* antennal retractor muscles are composed of extremely short sarcomeres and are likely among the fastest muscle fibers ever described. They also reported that the mean speed of antennal retractions in *Odontomachus* is twice as fast as recorded random movements of other ants including species that perform RA behavior (e.g. *Hapegnathos saltator*). However, these authors did not measure antennal movements happening during RA bouts. The physiology of *Odontomachus* may allow for faster RA and it would be worth repeating the approach of Ehmer and Gronenberg (1997) in other species that use RA to determine how strike frequency is correlated with muscular or neural characteristics of the antenna.

Three of the species described here *O. brunneus*, *O. ruginodis*, and *O. haematodus*, belong to a new world clade within the genus *Odontomachus* and are more closely related to one another than they are to *O. rixosus* which is part of a well-defined old-world clade (Schmidt 2009; Larabee et al. unpublished data). Ranked by body size, *O. ruginodis* is the smallest of our species followed by *O. brunneus* and *O. haematodus*, *O. rixosus* is the largest (MacGown et al. 2014). Of these species, *O. rixosus* is unique in its body proportions, being slender and long in body and antennal shape. Trade-offs between size and speed are common in appendages (Spagna et al. 2008; Emlen 2014), however, if RA rate were solely a product of body or antennae size, *O. ruginodis* would be predicted the fastest and *O. haematodus* should be slower than both *O. ruginodis* and *O. brunneus*. Although we have currently only sampled only four species, we predict that phylogenetic relationships among species may better represent variation in RA rate than body size.

Rapid antennation behavior is used in aggressive interactions between non-nestmates and in dominance interactions between nestmates in *O. brunneus* (Smith et al. 2013; Powell and Tschinkel 1999). Though RA has yet to be formally described as a dominance behavior between nestmates for *O. ruginodis*, *O. haematodus*, and *O. rixosus*, exchanges of RA between workers in the laboratory nests of all species is common for all of these species (personal observations of A.A.S and S.O.). Further studies are needed with these species to test the hypothesis that these RA behaviors between nestmates are dominance behaviors. Rapid antennation has also been described as a behavior of workers during intracolony conflict over reproduction (van Walsum et al. 1998) and a dominance behavior between nestmate queens (Medeiros et al. 1992) for other *Odontomachus* species. Our results indicate that when *O. brunneus* direct RA behaviors towards nestmates or non-nestmates, attributes of the behavior are not quantitatively different. The lack of a clear contextual difference in RA

behavior is not surprising. We hypothesize that differences in RA behavior are likely the result of selection on worker RA behavioral response thresholds rather than selection on diversifying specific attributes of the behavior to fit different contexts such as an aggressive response to a non-nestmate or an intracolony interaction. We therefore predict that workers will differ in the frequency in which they respond to nestmates and non-nestmates with RA behavior, rather than exhibit different RA characteristics (e.g. strikes/s) in response to nestmates and non-nestmates. A direct comparison of this has been previously made with *O. brunneus*. Smith et al. (2013) found that 19/24 non-nestmate pairing resulted in RA behavior, but only 9/24 random nestmate pairing resulted in RA behavior. Though we did not quantify this measurement in this study, RA bouts were more frequent between non-nestmates than between nestmates pairing for all of these species (authors' A.A.S. and S.O. personal observations).

The evolution of rapid antennation behavior is an interesting and largely unexplored area of social insect biology. It is a widespread behavior in social hymenoptera and our work suggests that it is easily observed and induced in an aggressive behavioral context and that those observations can correlate with how those behaviors are performed between nestmates. The clear differences and variability we found in RA rates between species, and what has been previously reported for *Polistes* wasps (Pratte and Jeanne 1984), suggests that phylogenetic comparisons of RA behavior could be informative. Future work in this area could lead to a better understanding of how aggressive behaviors evolve and are used inside the nest to organize social insect societies.

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