

Unsuccessful attacks dominate a drone-preying wasp's hunting performance near stingless bee nests

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ABSTRACT. Bee males (drones) of stingless bees tend to congregate near entrances of conspecific nests, where they wait for virgin queens that initiate their nuptial flight. We observed that the Neotropical solitary wasp *Trachypus boharti* (Hymenoptera, Cabronidae) specifically preys on males of the stingless bee *Scaptotrigona postica* (Hymenoptera, Apidae); these wasps captured up to 50 males per day near the entrance of a single hive. Over 90% of the wasp attacks were unsuccessful; such erroneous attacks often involved conspecific wasps and worker bees. After the capture of non-male prey, wasps almost immediately released these individuals unharmed and continued hunting. A simple behavioral experiment showed that at short distances wasps were not specifically attracted to *S. postica* males nor were they repelled by workers of the same species. Likely, short-range prey detection near the bees' nest is achieved mainly by vision whereas close-range prey recognition is based principally on chemical and/or mechanical cues. We argue that the dependence on the wasp's visual perception during attack and the crowded and dynamic hunting conditions caused wasps to make many preying attempts that failed. Two wasp-density-related factors,

wasp-prey distance and wasp-wasp encounters, may account for the fact that the highest male capture and unsuccessful wasp bee encounter rates occurred at intermediate wasp numbers.

Key words: Predation; *Trachypus*; *Scaptotrigona*; Male; Detection error; Wasp density

INTRODUCTION

Stingless bees are eusocial Hymenoptera occurring in tropical and subtropical regions of the world (Wilson, 1971). They are key pollinators of local plants (see Slaa et al., 2006) and produce highly appreciated honey (see Cortopassi-Laurino et al., 2006). Despite their importance, predation on species of this bee group has been poorly studied (see Roubik, 1989) and specific preying on reproductives is practically unknown.

As in other social hymenopterans, stingless bee males do not contribute to nest duties; their only role is to inseminate virgin queens (Sakagami, 1982). Males congregate near nests in clusters of a few to thousands of individuals (Engels and Engels, 1984; Roubik, 1989, 1990; Brown, 1997; Nogueira-Ferreira and Soares, 1998; but see Sommeijer and de Bruijn, 1995). These clusters apparently consist of males from multiple nests (Paxton, 2000; Cameron et al., 2004) and can last for several weeks (Engels and Engels, 1984). The males in these clusters wait for a virgin queen to leave the nest for its nuptial flight. There seems to be high costs associated with these congregations; lizards prey upon stationary *Scaptotrigona postica* males (Engels and Engels, 1984), and Brown (1997) reports that phorid flies parasitized 50% of clustered *Cephalotrigona capitata* males, while few workers were affected.

The sex ratio among reproductives in all stingless bees is heavily male-biased, and single mating is the rule (Peters et al., 1999); although some cases of double-mating of *S. postica* queens have been found by DNA analysis (Paxton, 2000; Paxton et al., 2003). Males in congregations may have a single mating opportunity or, most likely, none.

As in many *Trigona* species, *S. postica* guard workers bite intruders fiercely, while releasing an alarm pheromone to recruit nestmates to join in the defense of the nest (Schwarz, 1948). This pheromone is produced in the mandibular glands and, although this has not yet been specifically tested for *S. postica*, alcohols such as 2-heptanol and ketones are among the active substances (Luby et al., 1973; Johnson et al., 1985). Mandibular gland products also seem to play a role in *S. postica*'s foraging recruitment (Lindauer and Kerr, 1958, 1960; Schmidt et al., 2003). Male mandibular glands are relatively underdeveloped (Cruz-Landim and Fereirra, 1967).

Workers and males of *S. postica* are both black and virtually identical in size and shape. The exclusive predation by the wasp *Trachypus boharti* on *T. postica* males was previously observed by Giannotti and Pinto (2001). This way of preying is unique in that the wasps select between flying males and workers without provoking the aggressive defense behavior of the nest-guarding bees. How they achieve this is still an unsolved matter. We therefore studied the individual and collective hunting behavior of the wasps in front of *S. postica* nests and tested the wasps' chemical orientation towards *S. postica* males and workers. We found that most wasp attacks are unsuccessful and involve bee workers, though conspecific wasps are the most common target. Finally, we propose a mechanism of hunting used by wasp individuals in front of bee nests that can justify the distinctive, low rate of hunting success observed.

MATERIAL AND METHODS

Study site

Wasp hunting behavior was studied at the Aretuzina ranch, owned by Professor Paulo Nogueira Neto, which is located in the municipality of São Simão, São Paulo State, Brazil. Observations and experiments were performed during April and May 2003. The weather during these months presents the transition from Brazilian summer to winter; there are warm days with occasional rain and dry, and sunny days with lower temperatures, especially at night.

Study organisms: bees and wasps

All colonies of stingless bees stationed at this ranch are hived in wooden boxes with species-specific adaptations (see Nogueira-Neto, 1997). Each hive is uniquely coded with a letter and a number (Table 1). Sixteen hives of *S. postica* were placed in a more or less random arrangement in a large orchard. The predating wasp was identified as *T. boharti*.

Observation of wasp behavior

The observations on wasp behavior were concentrated on colony 17, where the number of wasps hovering in front was larger than at other colonies. Several wasps and their prey were collected by means of an insect net for identification. Specimens of wasps, captured males and workers of hive 17 were deposited in the collection of the Bee Laboratory of the University of São Paulo. Through direct observations, wasp presence and wasp attacks were recorded on three separate days from the early morning until all wasps left in the late afternoon. Wasp presence was estimated at intervals of 15 min, while attacks were registered continuously. For correlation tests, rate values were square-root transformed. Best-fit regression lines were selected on the basis of highest F-values.

Wasp abundance and prey capture

At the same hive, we studied the effect of wasp group size on prey capture on three different days by experimentally manipulating the numbers of wasps. This experiment consisted of three phases: 1) undisturbed hunting; 2) hunting following capture of about half of the wasps; 3) hunting after release of all wasps captured in phase 2. Each phase lasted 30 min; during the second phase of the experiment, the captured wasps were maintained in an insect net and protected from direct sunlight. Again, wasp presence was estimated at intervals of 15 min, while attacks were registered continuously.

Assessing abundance of wasps and male bees

During seven days we recorded at each bee hive the number of males near the hive shortly before the first wasps arrived and the number of wasps at the peak of hunting activity.

Chemical orientation of wasps to prey

An experiment was conducted to test whether wasps are attracted or repelled by *S. postica* males and workers. A closed, experimental setup was constructed of small plastic boxes (Figure 1). The setup consisted of a central space (dimensions: 10 x 10 x 3.5 cm) in which an individual wasp had to enter coming from the inside of a suction tube just after it had been captured in front of a hive. Two smaller boxes were connected to this box, which the wasp could enter. Each of these smaller boxes had dimensions of 5 x 10 x 3.5 cm and had either a 4-cm tube with four freshly caught, live bees or a similar, empty tube attached to it. A mesh filter separated the bees in the tube (and the empty tube) from the small choice boxes. The boxes were placed horizontally in a dark room and had a glass cover, which enabled us to observe wasp behavior and register it with a Sony video camera in night vision mode. The complete first entry of each wasp into one of the smaller boxes was recorded. Twenty wasps were given a choice between an empty tube and a tube with four workers. A second group of 20 wasps was given a choice between an empty tube and a tube with four males. Between trials, the glass cover and the insides of the boxes were cleaned and the tubes were switched. Wasps, as were bee workers and males, were freshly captured with an insect net while they were flying in front of hive 17. Each wasp was used once and was liberated at the end of a series of trials. Eight wasps were killed for further study and identification. Each group of four worker bees was used twice and immediately released after use. Males were used twice and were always released after a series of trials.

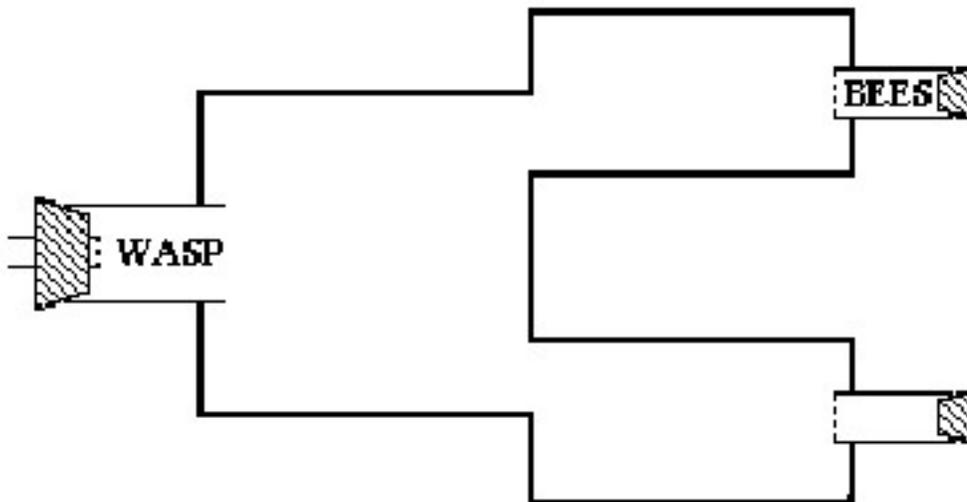


Figure 1. An illustration of the experimental setup used to test the chemical orientation of *Trachypus boharti* towards *Scaptotrigona postica* prey, seen from above.

RESULTS

Presence of wasps near *Scaptotrigona postica* hives

Trachypus boharti was encountered flying in front of various hives of *S. postica* (Table 1) during at least two successive months, from the middle of March to the middle of May. At times, more than 20 wasps were hovering in front of hive 17, while some other colonies had one to several wasps hovering in front. The number of wasps differed per colony and varied during the day. Before 10:00 am, no wasps were present at hive 17 or the other hives; bee foraging started some hours earlier. At about 10:00 am, the first wasps arrived at the bee colony; their numbers rose steadily until midday. Thereafter, wasp numbers dropped slowly, and at around 5:00 pm almost all wasps had disappeared. Foraging of *S. postica* workers continued for some time after the wasps left. The daily pattern of wasp presence was consistent over the three observation days. Wasps arrived earlier on warm days than on cool days, and no wasps arrived during rain. During the three observation days at hive 17, a mean of 11 wasps (range = 1-27; SE = 6.0; N = 79) were present during each 15-min period.

Exclusive preying on *Scaptotrigona postica* males

The wasps hovering in front of the *S. postica* hives regularly attacked flying bees. Inspection of intercepted wasps with prey showed that they exclusively captured males (N = 33). On three different days 47, 65, and 46 captures, respectively, were registered in front of hive 17. During a 15-min time frame, wasps captured an average of two males (range = 0-8; SD = 2.1; N = 79).

Generally, the wasps made short flight runs of less than a meter to and from in front of the hives, within a narrow plane more or less perpendicular to the hive entrance. Individual wasps flew in nearly horizontal tracks, intermittently shifting slowly up and down in wave-like movements. Attacks were clearly visible because the more or less horizontal flight pattern of a wasp was suddenly interrupted. During its attack, the wasp flew down, probably on top of its victim in an attempt to seize it. A wasp with a captured bee fell downward in a straight line, sometimes even for several tens of centimeters. Because all hives on the farm are on supports about a meter from the ground, the wasp and its prey occasionally hit the ground. When a wasp was able to get hold of its victim, it flew up slowly and carried its load away. A loaded wasp flew much more slowly than an unloaded wasp and could easily be intercepted. Among 21 wasp-male ensembles intercepted at hive 17 and among 12 wasp-male ensembles intercepted at hive 18, six and three males, respectively, were already paralyzed within seconds after being captured by the wasp. Immobilized males were found to be fully intact but characteristically had their wings widely spread and their tongue sticking out.

Wasps hunted mostly at hives with more than five males (Table 1; May 6, N = 15, P = 0.017; average of May 13-18, N = 16, P = 0.034; Fischer exact test). Just two hives (9 and 10) had a large number of males and hardly any wasps. In contrast, at one hive (14) males were seldom seen, but one or two wasps were regularly observed in front. The choice experiment showed that at a short distance wasps were not attracted to *S. postica*

males nor were they repelled by workers of that species (chi-square test, male:empty = 11:9 versus worker:empty = 7:13; $P = 0.2$; $\chi^2 = 1.63$). Wasp choice was independent of box position (left box: 24, right box: 16; $P = 0.37$; $\chi^2 = 0.81$).

Table 1. The presence of males on or near 16 *Scaptotrigona postica* hives and the occurrence of hunting wasps.

	Date	Colony															
		1	3	4	5	9	10	11	12	13	14	15	16	17	18	21	D1
Male numbers	May 6	2	6	2	2	4	15	6	3	?	0	0	0	7	2	2	14
Wasp presence			x					x			x			x			x
Male numbers	May 13	2	0	2	0	3	10	2	2	13	1	0	0	8	8	0	3
	May 14	0	0	2	3	6	19	0	17	38	0	1	0	18	42.5	3	10
	May 15	5	0	0	0	2	7	2	1	55	1	1	0	5	60	1	2
	May 16	7	0	1	0	10	8	0	0	42.5	0	0	0	4	55	5	18
	May 17	1	0	3	0	47.5	13	3	0	24	0	0	0	5	55	2	6
	May 18	2	0	0	0	34	3	0	1	11	0	0	0	1	42.5	8	3
Mean		2.7	0.9	1.4	0.7	15.2	10.7	1.9	3.4	30.6	0.3	0.3	0.0	6.9	37.9	3.0	8.0
Wasp presence										x	x			x	x		x

On May 6, which began cloudy and had only sunshine in the afternoon, *S. postica* males were noticed resting on the hives, while almost no wasps were encountered. That day, males resting on or near hives were counted at around 2 pm in order to correlate their presence with the general pattern in which wasps appeared at individual hives over the following weeks. Male counts were made at 11 am every day from May 13-18. During these early mornings, wasp numbers were still low. In parallel, the daily presence of wasps in front of hives was noted. All bee colonies (1-21) were identified as *S. postica*, except D1, which may have been a mixture between *S. postica* and *S. depilis*.

Hunting success and the effect of wasp density

We observed 2271 wasp attacks; in 7.0% of these a male was successfully captured. The remaining attacks were unsuccessful wasp-bee attacks (24.7%) and wasp-wasp interactions (68.3%). It could not be determined whether or not the unsuccessful attacks on bees involved *S. postica* workers or males. In wasp-wasp attacks, both wasps often fell down, as in wasp-bee attacks. After a drop, they always separated and both continued hunting.

Male capture rate by wasps was two times higher at intermediate levels of wasp density than at very low or very high density (Figure 2A; quadratic regression: $F_{(2,40)} = 11.42$; $P < 0.001$). The number of unsuccessful wasp-bee attacks revealed a similar pattern (Figure 2B; quadratic regression: $F_{(2,40)} = 6.04$; $P < 0.01$), whereas wasp-wasp attacks increased logarithmically with increasing numbers of wasps ($F_{(1,41)} = 58.2$; $P < 0.001$; Figure 2C). Experimental reduction of wasp numbers resulted in no change in the per capita male capture rate (Figure 3A; chi-square test: all $P > 0.2$). This non-significance may be due to the low numbers of males captured during the experiments, although these numbers were within the range of captures per 15 min registered during the three days of continuous observations at hive 17. The same experiment resulted in both lower and higher total numbers of unsuccessful attacks proportionate to the number of wasps, but these changes were non-significant (Figure 3B; $P > 0.5$; chi-square test).

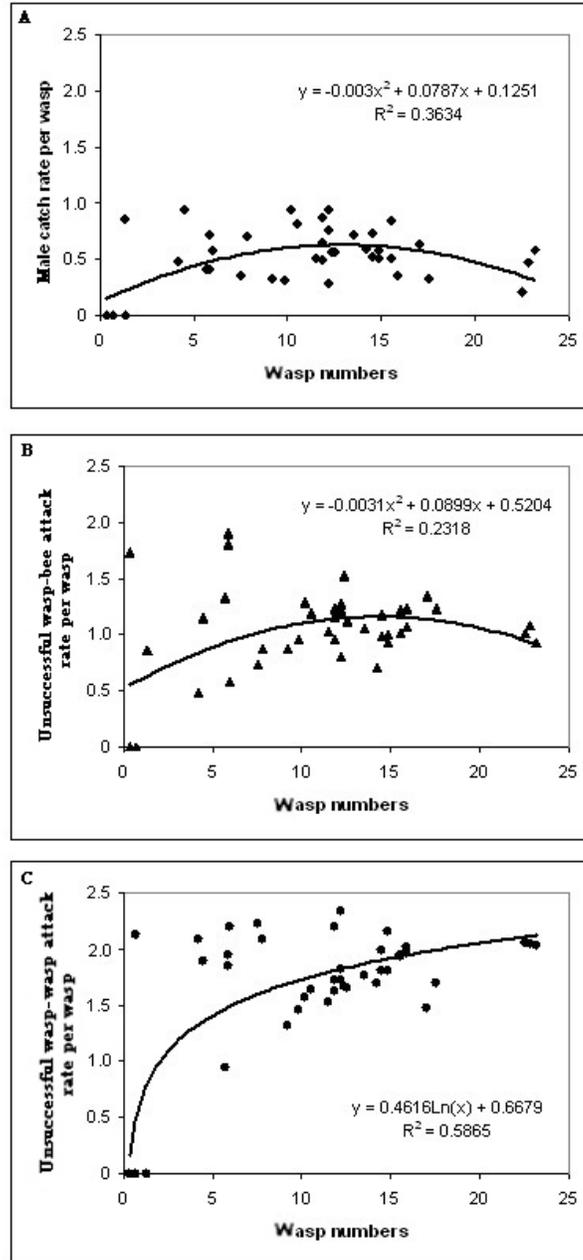


Figure 2. Correlations between **A.** *Trachypus boharti* wasp density and *Scaptotrigona postica* male capture rate per wasp; **B.** Wasp density and the rate of unsuccessful bee attacks per wasp, and **C.** Wasp density and the rate of unsuccessful wasp attacks per wasp. See text for the procedures of behavioral observations. Data points represent wasp density and attacks per half hour of observation and inserted texts depict best fit and corresponding R-squared. The continuous observations of wasp behavior during three days at hive 17 were subdivided into units of 30 min. Wasp numbers were subsequently averaged over three subsequent 15-min interval estimates, one at the beginning, one in the middle and one at the end of a 30-min period; during the same period wasp attacks were summed. Unsuccessful attacks were split up into wasp-bee attacks and wasp-wasp attacks. For correlation tests, rate values were square-root transformed. Best-fit regression lines were selected on the basis of highest F-values.

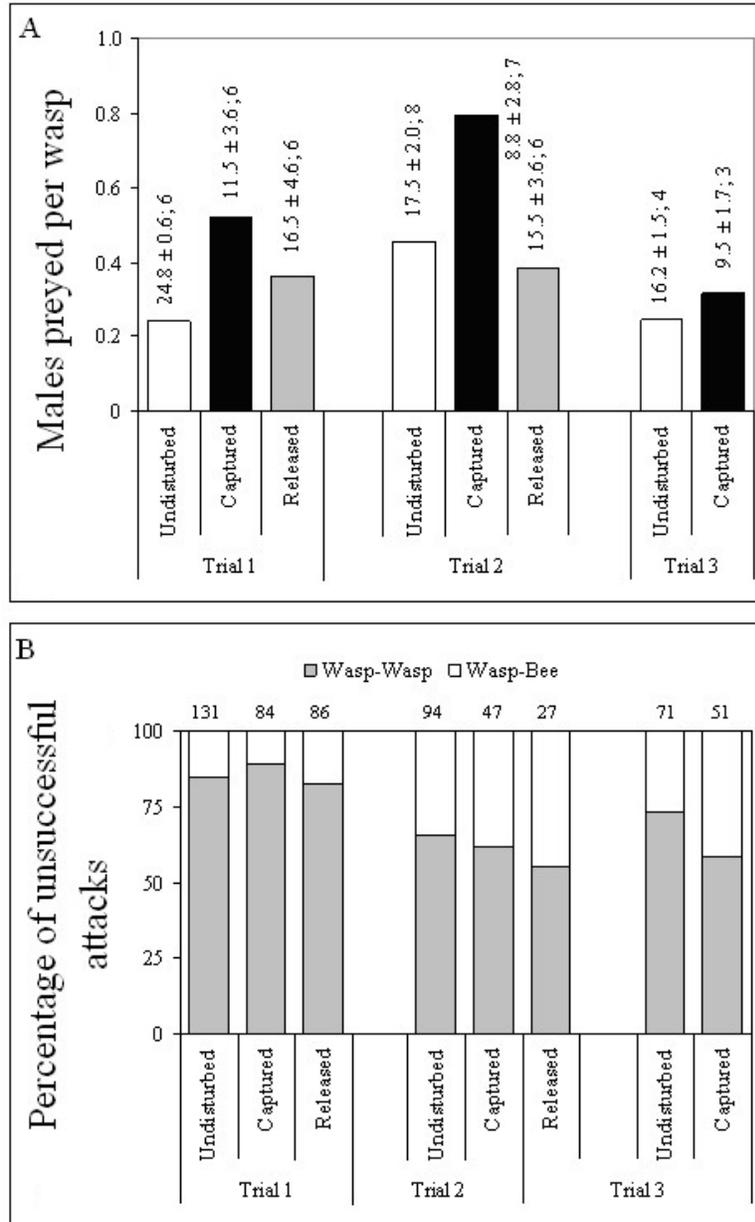


Figure 3. Effects of the experimental manipulation of wasp numbers on **A**. The number of male captures and **B**. The number of unsuccessful attacks. See text for the experimental procedure. Above bars: in *A*. Numbers of wasps averaged (\pm SD) over three counts made at the start, middle, and end of a test phase, followed by total numbers of captured males for that phase, in *B*. Numbers of unsuccessful attacks totaled for a test phase. The manipulation of wasp numbers consisted of three trials, each executed on a different day. Trial 3 was ended prematurely by the arrival of many hovering *Tetragonisca angustula* stingless bees from a nearby colony.

DISCUSSION

Exclusive male bee catch by a Neotropical wasp

As previously reported by Giannotti and Pinto (2001), we found the wasp *T. boharti* exclusively preys on males of *S. postica* and not on the reproductive females or worker bees of this species. This does not of course prove that it does not hunt other insects elsewhere.

We found that wasps captured more than 50 males a day at a single colony and that hunting persisted for more than two months. This amounts to a capture of about 3000 males in front of that colony alone, which suggests a high cost of male aggregation. Nevertheless, *S. postica* males probably have no other option than to gather near nests having virgin queens and wait for a mating opportunity. As yet, we have been unable to determine if the bees adopted some kind of anti-predation strategy to lower wasp predation pressure.

Most other bee-hunting philanthine digger wasps hunt female bees at flowers (Tinbergen, 1932; Evans and Matthews, 1973), although some species of both *Palarus* (*Larrinae*) and *Philanthus* (e.g., *P. triangulum*, *P. gibbosus*) are known to take prey at bee colonies (Simonthomas and Simonthomas, 1977, 1980; Clauss, 1985). *Trachypus boharti*'s hunting site is always near the entrance of nests of the species it preys on; in our case, wasp activity was monitored at a semi-natural assemblage of *S. postica* nests. We believe that this setting, which in a certain way aided in obtaining the necessary data for this paper, did not interfere with the normal conduct of these species. Firstly, *S. postica* belongs to one of the most common bee genera of Brazil (Ramalho, 1995) and has large nests (Lindauer and Kerr, 1960). Secondly, stingless bee nests are estimated to survive more than 20 years (Slaa, 2006). This must be true for *S. postica*, given that it, as is also found for *S. pectoralis* (Slaa, 2006), is normally found nesting in relatively large trees with a large trunk diameter (data not shown). Thirdly, *S. postica* males are produced throughout the year (Bego, 1982) and, in the case of strong colonies, congregations of males at a single nest can persist for many weeks (Engels and Engels, 1984; this study). Therefore, the frequency of nests, the size, persistence, and recurring presence of male congregations may have allowed this wasp to specialize on the males of this species.

Low rates of hunting success and prey detection error

We found that the wasps' rate of success was generally very low, being on average 7.0%. Most of the erroneous attacks involved other wasps. Although at times there were large numbers of wasps at a hive, wasp-wasp attacks were already common at relatively low wasp densities (Figure 2C). For instance, five wasps at the same nest entrance could carry out more than 10 of these erroneous strikes in just half an hour. Although most wasp predation attempts involved other wasps, such attacks never escalated into real fights; when wasps interfered with one another, both the course of interference and its short duration were similar to the cases in which a wasp seized a bee but freed it soon thereafter. Moreover, wasps did not expel each other from the hunting site as happens with another bee predator, *Vespa velutina* (Tan et al., 2007). Our observations therefore appear to indicate that wasps scramble for males and that wasp-wasp attacks are likely the result of a kind of prey detection error.

The many erroneous attacks on conspecifics make it likely that the wasps also targeted *S. postica* workers on a regular basis. However, the hunting wasps apparently never triggered

collective defense and alert behavior of this bee, although we were sometimes attacked at several meters distance from the bees' nest. After unsuccessful wasp-bee attacks, the wasps sometimes retreated to a leaf several meters from the bee nest where they vigorously groomed their body. It may be that in such cases a worker bee successfully countered the attack by biting or applying alarm pheromone.

Comparing predation by *Philantus triangulum* and *Trachypus boharti*

A comparison with what is known about the European beewolf, *Philantus triangulum* could provide insight into how *T. boharti* hunts prey. *Philantus triangulum* is specialized on honey bees and hunts in the open field at flower patches that are visited by wild bees and other insects (Tinbergen, 1935). It can visually perceive its potential prey within a distance of about 30 cm. Before attacking, a wasp evaluates the scent of the individual during a phase in which it hovers almost still in the air (Tinbergen, 1935). Whenever the odor is not suitable, the wasp aborts its attack. When the odor is that of a honey bee, the wasp starts its rapid approach, the so-called dart, which is purely visually guided. Occasionally, while darting, the honey bee worker originally aimed at can suddenly leave the wasp's range of vision while another insect can simultaneously enter it. In such cases the wasp will proceed with its darting, but it will be directed towards an individual that may not be a honey bee. When the swapped individual is not a honey bee, the wasp may eventually grab it but rapidly perceive its error and let it go instantly. Sporadic darting by *P. triangulum* at non-bee insects and bees other than honey bees demonstrates that this wasp's visual system keeps track of the location of its prey rather than of its shape and color.

Some aspects of the way *T. boharti* wasps target their victims and discriminate prey from non-prey are likely to be similar to the hunting mechanism of *P. triangulum*. Others, like *P. triangulum*'s distinct phases of hovering followed by darting, seem absent although video recording would help to check this issue. The chasing of worker bees and of conspecifics, yellow and about 2-fold the size of the bees, could indicate that, similar to *P. triangulum*, *T. boharti* wasps focus visually on the position of prey and also largely disregard information about what the prey looks like. We found that over a short distance wasps are not chemically attracted to *S. postica* males, but this does not exclude the possibility that under natural conditions every time a wasp localizes a potential prey, it first has to smell or taste it to assess whether or not to continue its attack. Recently, it has been determined that the cuticular hydrocarbons that *S. postica* bees possess are sex-specific (Koedam D, Morgan ED, Patricio EFLRA and Imperatriz-Fonseca VL, unpublished results). Tests are underway to verify whether or not these cuticular substances individually or as a mixture serve as a recognition cue for wasps during hunting.

A *T. boharti* wasp's prey selection seems to operate when it is very close by or is in contact with the individual it attacks. Of course, the use of tactile stimuli should also be taken into consideration when wasps are within reach of their target. For instance, in the cases of attacks on workers, their defensive biting may be a cue for wasps to release the workers.

We suppose that the occurrence of unsuccessful attacks is due to accidental swapping of prey for non-prey within a wasp's range of vision as it occurs during a *P. triangulum* wasp's launch of attack. Bee traffic in front of *Scaptotrigona* nests is always intense (Biesmeijer et al., 2007) and wasp numbers can sometimes also be quite high (this study). One should realize that the wasps hunt inside a small cloud made up of up to more than a hundred bees constantly flying around. This signifies that at any given moment wasps fly within a distance of up to

about 50 cm of several different bees all heading in various directions. It is therefore expected that due to crowded and dynamic conditions in front of *S. postica* nests prey swapping is the rule rather than the exception. This fact may explain why an extremely large proportion of *T. boharti* preying attempts failed.

Wasp density, wasp-wasp attacks and hunting success

All regressions gave low r^2 values and high variance in the independent variable. Variance in hunting success may have been due to the generally few male catches per time unit. Overall, hunting opportunities may have been affected by small shifts in bee numbers and local weather conditions, such as wind speed and direction, and luminosity. As the experimental removal of wasps was done at the same hive, these same factors may have added to its non-significant and sometimes mixed outcomes.

Wasp numbers seem to affect both the encounters with bees and hunting success in ways that, depending on their density, are opposite to each other (Figure 2A,B). On the other hand, with increasing wasp density, wasp-wasp encounters rise sharply, whereupon their numbers asymptotically approach a maximum value (Figure 2C). Here we try to interpret the course of these regression equations.

Firstly, it is fair to state that the space the bees and the hunting wasps occupy is roughly limited in size. Except for localized clumping immediately in front of the nest entrance due to outgoing and incoming foragers, it is likely that the rest of the swarm individuals are to a large extent evenly dispersed. This implies that with every extra individual, the swarm gets denser and the average distance among individuals is reduced. So, with an increase in wasp density, all wasps will get a little closer to bees and to each other. This compacting will increase their success in catching males but likewise will increase the number of unsuccessful attacks. The left-hand sides of Figure 2A,B, and C reveal this pattern; at low wasp density, every extra wasp increases wasp-bee and wasp-wasp encounters per wasp and thus also raises their success rate.

Secondly, the normal occurrence of attacks on non-prey, especially conspecifics, makes every wasp, in contrast to a bee, both a hunter and a potential target. This means that, with every extra wasp in front of an *S. postica*'s nest, the total number of attacks will theoretically increase with a value that is equal to double the number of wasps already present. In practice, this means that when wasp density increases, the frequency of aggressive encounters between wasps initially increases significantly more than the frequency of encounters between wasps and bees (Figure 2A,B,C). Furthermore, each wasp can only launch a limited number of attacks per time unit, even when attacks are unsuccessful and therefore of relative short duration. Also, when the frequency of wasp-wasp encounters surpasses a critical point, these encounters must be at the expense of wasp-bee encounters. All this means that the rate of wasp-wasp encounters probably should not increase continually, but should gradually diminish and reach an asymptote (Figure 2C). It also implies that at the same high wasp density the number of wasp-bee encounters, as opposed to wasp-wasp encounters, drops and, as a result, the wasps' hunting success declines in a similar fashion (Figure 2A,B).

In short, every extra wasp would not only reduce wasp-prey distance and give wasps more success, it would also relatively rapidly increase the number of unsuccessful wasp-wasp attacks, which, at a certain wasp-density level, would provide wasps too little time left to encounter bees. This could explain why the highest unsuccessful wasp-bee encounter and male

capture rates occurred at intermediate wasp numbers; however, more research is needed to verify whether our notion is correct.

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