

Observations on colony defense of *Apis nuluensis* Tingek, Koeniger and Koeniger, 1996 and predatory behavior of the hornet, *Vespa multimaculata* Pérez, 1910

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Summary — Colony defense and predatory behavior of *Vespa multimaculata* was observed at the entrance of a natural nest site of *Apis nuluensis*. When *V multimaculata* was present, guard bees frequently performed body shaking behavior: bees lifted the tip of the abdomen slightly spreading the wings and exposed the Nasonov gland. The oscillation of the abdomen tip had an amplitude of 83° (SD = 50°; $n = 84$) and its duration was 0.08 s (SD = 0.01; $n = 84$). The individual behavior resulted in the rapid formation of a group of guard bees and induced body shaking of neighboring bees. The hunting *V multimaculata* workers hovered about 5–10 cm in front of the nest and blocked the direct flight path of bees returning to the nest. Returning foragers are regularly diverted from the nest entrances and attracted to the body shaking guard bees where they land beyond the reach of hovering *V multimaculata*. In contrast to *Apis cerana*, *A nuluensis* exposes its Nasonov gland during body shaking. During a period of 12 h one *V multimaculata* worker caught 14 bees. At the end of the observation we brought the hornet (tethered to a wire) into contact with a group of bees at the nest entrance. The *A nuluensis* guard bees immediately balled and killed the hornet with heat.

***Apis nuluensis* / *Vespa* / behavior / defense / predation**

INTRODUCTION

Colony defense of Asian *Apis* species is characterized by several distinct behavioral elements, which are absent in the western honey bee *Apis mellifera*. Unfortunately, some early observers reported reactions to

disturbances that were confounded with multiple stimuli, and a mixture of different behavioral patterns was described. For example 'shimmering' was described by Butler (1954) as a combination of body movements and a hissing sound: "When a hornet, ant or wax moth or any other intruder

approaches their nests they shake their bodies violently from side to side in concert, a behavior which I have called 'shimmering'.....a peculiar hissing sound accompanies the shimmering behavior of *Apis cerana*." Sakagami (1960) differentiated between the sound production for which he claimed the term 'shimmering' and his newly described 'abdomen shaking'. Schneider and Kloft (1971) analyzed a 'body shaking (Körperschütteln)' in *A cerana*. Later, Fuchs and Koeniger (1974) demonstrated that the hissing behavior in *A cerana* was released by mechanical stimuli. 'Body shaking' however depends on visual stimuli and commonly occurs when flying hornets approach the nest or the nest entrance (Schneider and Kloft, 1971; Koeniger and Fuchs, 1975).

The larger vespine wasps of the genus *Vespa* play a major role among the predators of Asian honey bees (Matsuura, 1988). Commonly, a hunting *Vespa* worker patrols in slow flight among flowers or other places where honey bees occur. Once a bee is located, the hunting hornet rushes forward to seize the bee. As a consequence, honey bees of the tropics and of other regions where hornets occur are very timid on their floral visits and react to the slightest disturbance by rapid retreat.

A more specific hunting technique was reported recently for *Vespa affinis*. These hornets flew in a drone congregation area and attracted drones of *A cerana*. The drones followed the hornet. The hornet then rushed at one of the drones and, after successfully seizing it, the hornet left the drone congregation area carrying away its prey. Apparently *V affinis* 'exploits' the intraspecific communication between queen and drones of *A cerana*, an example of predatory mimicry (Koeniger et al, 1994).

A cerana performs a specific group defense behavior at the entrance of the nest (Schneider and Kloft, 1971). In response to an approaching *Vespa* the bees perform body shaking behavior (Körperschütteln),

join together in a tight group, and maintain close contact. When the hornet attacks one group member, some will immediately cling to their nest mates, while others rush to surround the predator with a ball of bees. In this situation, the bees do not attempt to sting, but kill the hornet by raising their body temperature above 45 °C until the wasp is dead (Ono et al, 1987, 1995).

Recently a new cavity dwelling species of honey bee from the mountain areas of Borneo, *Apis nuluensis*, was described (Tingek et al, 1996). Here we report the first observations on the defensive behavior of *A nuluensis* at the colony entrance and how *Vespa multimaculata* circumvents this defense system.

MATERIALS AND METHODS

A colony of *A nuluensis* was found opposite the Gunung Emas rest house which is situated at the road which connects Kota Kinabalu and Tambunan (54 km from Kota Kinabalu). The hollow tree in which the colony had built its nest was situated about 150 m above the rest house at a steep slope in an elevation of 2 040 m. The only entrance to the nest was about 1.6 m above the ground. The temperature range was from 15 °C at 0800 hours to about 18 °C at 12 00 hours. In the early afternoon 20 °C was reached only during short intervals of sunshine. The sky was cloudy with intermittent light drizzle during the morning hours between 0800 and 1000 hours.

We watched the nest entrance from a distance of 1 m for 2 days (28/2/95, 1/3/95) from 0800 to 1600 hours and on 23/2/95 from 1100 to 1500 hours.

Defensive behavior of the bees at the nest entrance and preying *V multimaculata* workers were observed and video taped at the nest site. The analysis of body shaking behavior was based on video recordings with a Super VHS Camcorder (Blaupunkt C680). The use of a Panasonic AG 7355 VCR for playback enabled us to use half-frame analysis, so the presented data have a sampling rate of 50 frames per second.

In a single-frame analysis, video images were transferred to a digitizer and measured using interactive software (VideoPad). All lengths mentioned in the text are derived from the average wing length (8.09 mm; morphometric database of Institut für Bienenkunde), which was used for calibration of the video scaling. In the first frame of every analyzed sequence, the size and orientation of the bee were obtained by fixing the wing tip, the wing insertion, the head, the center of the thorax and the tip of the abdomen. Positions of the head, thorax and abdomen were used as initial values for measurements of dislocations during the sequence. Amplitudes of the oscillations refer to the initial orientation of the body axis, defined by the positions of the head and the tip of the abdomen.

For identification we caught the *V multimaculata* worker with an insect net and marked it with a pink dot on the thorax. To investigate worker responses to direct contact with *V multimaculata* at the end of our observations, we caught the hornet again and fixed it to a wire which was bent around the petiolus. The tethered hornet was brought into contact with a group of workers on the tree's surface, near the nest entrance. The specimen was identified as *V multimaculata* according to van der Vecht (1957) and sent to Tamagawa University, Japan, for confirmation of identification.

RESULTS

Analysis of body shaking in A nuluensis

The body shaking behavior of *A nuluensis* is a specific repetitive pattern of movements which are characterized by shaking intensity and duration. When stimulated (here the presence of a hovering hornet) the guard bees start performing a body shaking pattern every 1.01 ± 0.17 s ($n = 102$). At the beginning of each pattern, the bee lifts the tip of the abdomen slightly spreading her wings and exposes the Nasonov gland. The tarsi are fixed on the substrate and the feet are kept in constant position while the whole body starts swinging from side to side. Head and thorax move with low amplitude but the tip of the abdomen is dislocated up to 10 mm from its initial position. Figure 1 gives an example of a movement pattern with three oscillations and a maximal dislocation of 6.6 mm. Thus the body shaking can be characterized by the swinging movement of the abdomen around the fairly stable tho-

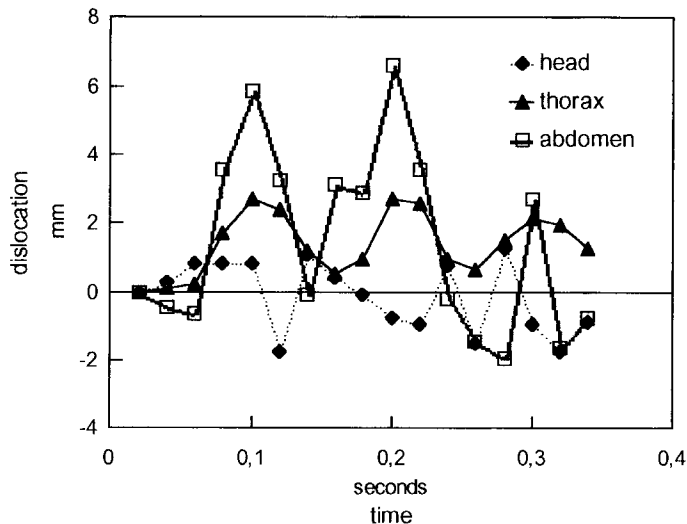


Fig 1. Sample diagram of movement pattern of *A nuluensis* body shaking. Dislocation of the head (◆), thorax (▲) and tip of the abdomen (◻) are expressed in lateral deviations (in mm) from the initial position.

rax, which resembles the observer's visual impression of a delta shaped visual pattern during the shaking sequence (fig 2). The oscillation of the tip of the abdomen has an amplitude (lowest extreme to highest extreme) of 83° (SD = 50°; n = 84) and its duration is 0.08 s (SD = 0.01 s; n = 84).

On average, a shaking pattern consists of 2.4 oscillations, but 59% of the observed workers (N = 34) performed two whole oscillations or less (fig 3). After the second oscillation the amplitude decreased significantly (fig 1). Even though single worker bees perform body shaking, most frequently the indi-

vidual behavior resulted in a rapid formation of a group of workers. A remarkable coordination of the individual's body shaking occurred when ten or more bees assembled at the trunk near the nest entrance. Usually a single worker started body shaking, thus inducing neighboring bees to do the same. This reaction continued in a wave-like movement of the whole group. The stimulus for each bee to start was transmitted within the group with a speed of about 1 m/s (estimated). Interferences of different 'wavefronts' originating from different starter bees also occurred.

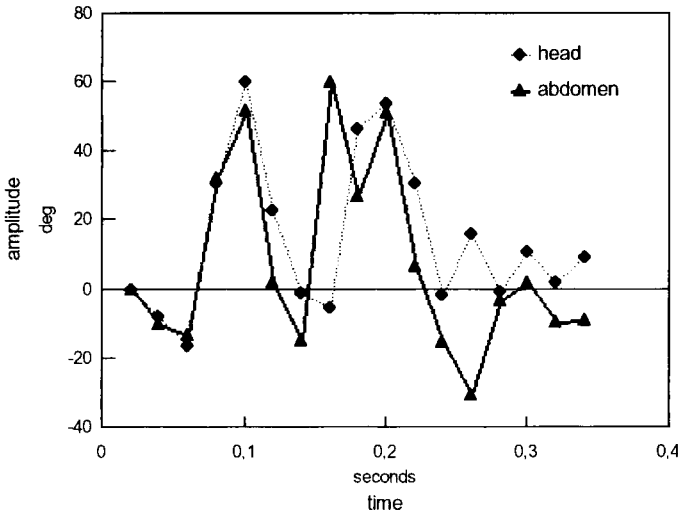


Fig 2. Sample diagram of movement pattern of *A. nuluensis* body shaking. Dislocation of head (◆) and tip of abdomen (▲) are expressed as angular deviations from the guard bee's initial body axis.

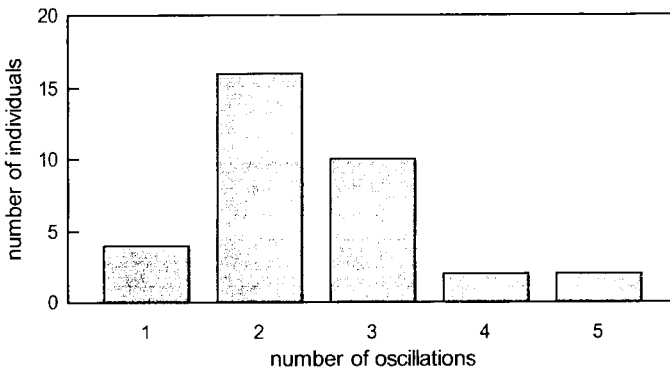


Fig 3. Oscillations per cycle of body shaking behavior. The number varies from a single to five oscillations. The majority of guard bees (76%, n = 34) perform either two or three oscillations.

Control observations: behavior at the 'undisturbed' nest entrance

During the periods without any obvious disturbances by predators or larger moving objects, two to six worker bees were patrolling more or less solitarily on the outer portion of tree trunk's mossy bark near the nest entrance (fig 4). These bees frequently stopped running and started fanning. From time to time one of the bees would take off from there. Several of these bees disappeared in the dense vegetation. In a few cases only, a short flight around the tree and in the very near surrounding (which we could follow with our eyes) was undertaken before the bee returned into the nest. During most of our observation time there was high foraging activity. We counted 25 to 33 returning bees per minute. About 60 to 70% of the returning bees were carrying pollen loads. The bees flew straight into the niche (the entrance to the nest was a hole in the bottom of this niche), landed near to the entrance and rapidly disappeared into the nest. Departing bees crawled out from the

entrance hole for 2–6 cm and then took off, leaving in a straight and mostly upward flight path.

Recruiting of guard bees

We observed an immediate reaction when a preying hornet (*V. multimaculata*) arrived at the nest entrance. The number of bees guarding the outer side of the tree's surface increased rapidly. A single episode observed is reported here. At the arrival of the hornet two bees were in front of the nest entrance on the outer side of the tree. Immediately, these two bees started body shaking behavior. One minute later, several bees from the nest had joined them. They formed a group of 13 bees that were engaged in intensive body shaking behavior, which was interrupted by short intervals during which the bees changed positions within the group. After 2 min, the group number had grown to 20 bees and 5 min later 32 bees were counted in two groups. This number remained more or less constant (28–35).

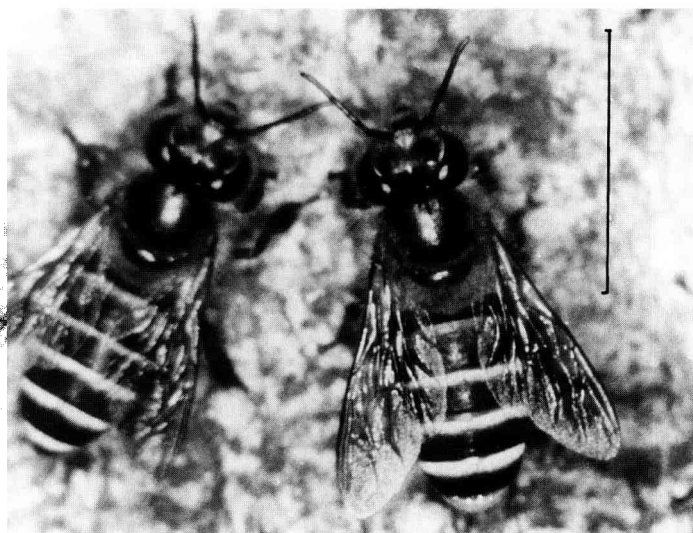


Fig 4. Guard bees of *A. nuluensis* near the nest entrance. Bar = 1 cm.

The hornet left after 12 min of hovering, then the body shaking behavior stopped and the number of guards decreased again to two or eight bees. In four other periods we counted a similar increase of guard bees on the tree trunk after the hovering hornet had appeared to groups ranging from 25 to 48 bees. Apparently, the recruitment of guard bees, the formation of a group and the maintenance of the group was always accompanied by 'body shaking' behavior.

Goal keeper's behavior

The *V. multimaculata* workers hovered about 5–10 cm in front of the nest in a more or less stationary position (fig 5 a). During this time, the hornet kept the nest entrance more or less to its back and maintained its body axis directed towards the outside. Thus, the hovering hornet blocked the direct flight path of homing bees into the nest and guarded the entrance of the bee colony. When a returning bee approached, the hornet reacted by stretching and spreading the legs (fig 5b). Fast turns and position changes towards the incoming bee were frequently performed (fig 5c). The average duration of this stationary hovering phase was about 30 s ($n = 25$, $sd = 16$ s) and the hornet could stay for as long as 72 s before it changed to the next hovering position. Because of obvious superficial similarity with the goal keeper in a game of soccer we suggest the term 'goal keeper's behavior' for this hunting technique of *V. multimaculata*.

Reactions of returning forager bees

In case of the presence of a preying *V. multimaculata*, the bees came in with high speed and straight flight. Based on video recordings we estimated the bee's speed was about 4–7 m/s at a distance of 50 cm from the landing position. Further, the bees

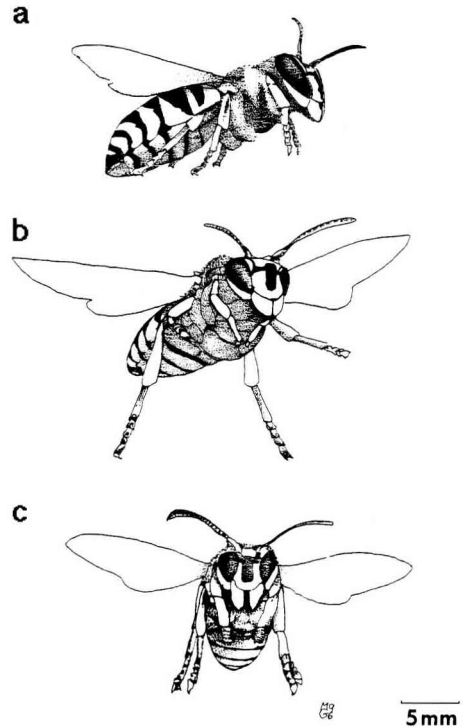


Fig 5. *Vespa multimaculata* ambushes returning foragers. **a.** The *V. multimaculata* workers hovered in a more or less stationary position. **b.** When a returning bee approached, the hornet reacted by stretching and spreading the legs. **c.** Fast turns and position changes towards the incoming bee were frequently performed.

tried to avoid the hornet by landing outside on the tree trunk beyond the hovering hornet's reach. Frequently they touched down near to the group of body shaking guard bees and from there they finished the last few centimeters of their journey to the nest with a fast run. The hornet did not react to bees after they landed. We did not notice any reaction of the hornet to bees moving on the surface or performing body shaking behavior. Also, bees flying out from the nest passed the hornet from behind and rarely elicited any position changes or catching reaction of the hovering hornet. In one case

an out-flying forager collided with the hornet without getting caught.

Killing of the captured bee

When a hornet successfully grasped an incoming bee, both would fall for about 1 m. Then the hornet would start to fly and land carrying the bee on a leaf or branch nearby. There the hornet took hold by its third pair of legs and would hang in a head downward position. The buzzing bee was then handled by the hornet's legs (pairs 1 and 2); it was turned around until the hornet could reach the bee's head and neck by its mandibles. About 2–5 s later, the bee's head was chewed off and fell down. The hornet would leave carrying the headless prey away. Because of the dense vegetation we could not follow the hornet.

Territorial behavior of preying V multimaculata

On our first day of observation we saw two *V multimaculata* workers hovering at the nest entrance of the colony. Between these hovering hornets we saw some approaches and very short aerial contacts, which appeared to be of an aggressive nature. The larger hornet then remained in front of the nest entrance while the smaller one hovered in an area peripheral to the nest, retreating whenever the other hornet approached. The following days observations were made with one hornet only, which we marked with a pink dot on the thorax and watched for 2 days.

Predatory success

There were 14 successful catches during an observation period of 12 h (2 days). In one further attempt the hornet lost the bee

after a first grabbing contact. On average the hornet arrived about 6.5 min (sd = 4.4) before the catch and returned 14 min (sd = 5.3) after it had left with prey. Unsuccessful hornets stayed for an average period of 7.5 min (sd = 4.8) at the bee's nest before they left.

Balling behavior of A nuluensis

At the end of the observation we caught the hornet with an insect net and carefully fixed a wire around its petiolus. Then we brought the fixed hornet into contact with a group of bees at the nest entrance. At once these bees balled the hornet and more and more bees rushed out of the nest and joined the ball. When we removed it after 20 min by pulling the wire about 40 bees clung to the hornet (fig 6). Since no temperature measuring device was available we followed the example of Ono et al (1995) and placed the bee ball on the observer's (NK) hand. The temperature was high, distinctly above 37 °C and neither the bees nor the hornet stung. We kept the wire swinging in the air for another 10 min before we removed the bees and we saw no motility of the hornet any more. So, in our case, the total duration of the ball was 30 min, which was apparently sufficient to kill *V multimaculata*.

DISCUSSION

The analysis of body shaking movement of *A nuluensis* revealed several similarities to *A cerana* (table 1) and the details of additional movements of *A nuluensis* were similar to earlier descriptions of *A cerana* (Schneider and Kloft, 1971; Koeniger and Fuchs, 1975).

Both *Apis* species perform body shaking behavior at the nest entrance as a group defense against predatory hornets and, thus, the function of body shaking seems to be

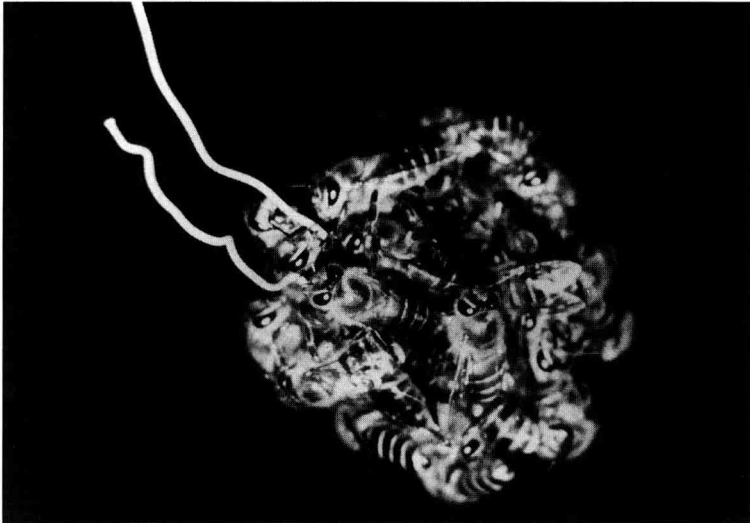


Fig 6. *A nuluensis* guard bees balling a hornet which was tethered to wire. When the ball was removed from the nest entrance about 40 bees clinged to the hornet which was killed with heat.

the same: to prevent intruding flying insects from landing (Koeniger and Fuchs, 1975).

Typically, preying *Vespa* workers do not attack flying bees; rather they successfully pick up single bees from the substrate near the hive entrance. As a counter strategy *A cerana* seems to have evolved a group defense. As soon as a hornet appears, bees join together in tight groups performing body shaking. This behavior wards off hornets (Schneider and Kloft, 1971). In case of a hornet attacking the group, bees cling together and kill the hornet by balling. This is also performed by *Apis nuluensis* as the

experiment with the tethered hornet indicates.

Hunting *V multimaculata* workers, however, stay away from bees moving on the substrate. They ambush by hovering in front of the nest entrance catching returning foragers (like a goal keeper in front of his goal catches a flying soccer ball). The counter strategy of *A nuluensis* against this hunting technique seems to depend on a significant variation of body shaking behavior. In contrast to *A cerana*, *A nuluensis* exposes its Nasonov gland during body shaking. The pheromones of this gland attract bees (Free,

Table I. Comparison of body shaking of *A cerana* and *A nuluensis* (the data for *A cerana* are from Schneider and Kloft, 1971).

	Duration of oscillation (s)	Amplitude of oscillation (°)	Number of oscillations
<i>A cerana</i>	0.09	79	2
<i>A nuluensis</i>	0.08	83	2.4

1987). So it may increase the recruiting effect of body shaking behavior and, furthermore, returning foragers are diverged from the nest entrance (which is guarded by the hovering predator) and attracted to the body shaking guard bees where they touch down regularly. Nevertheless the preying success of one *V multimaclata* worker was 14 bees during 12 h.

The territorial behavior of preying hornets seemed to result in excluding additional hornets from the nest entrance and might prevent a more severe exploitation of an *A nuluensis* colony. This might further contribute to a limitation of damaging effects and to the survival of the bee colony. These speculations however need to be confirmed by long term observations on more *A nuluensis* colonies and predatory *V multimaclata*.

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Résumé — Observations sur le comportement de défense d'*Apis nuluensis* Tingek, Koeniger et Koeniger, 1996 et comportement prédateur du frelon *Vespa multimaclata* Pérez, 1910. Le comportement de défense d'*Apis nuluensis* et le comportement prédateur de *Vespa multimaclata* ont été observés et enregistrés avec une caméra vidéo à l'entrée du site de nidification d'*A nuluensis*. En présence de *V multimaclata* les abeilles gardiennes exécutaient un tremblement du corps toutes les $1,01 \pm 0,17$ ($n = 102$) secondes. Au début de

chaque séquence l'abeille soulève légèrement l'extrémité de son abdomen, étend ses ailes et expose sa glande de Nasonov. L'oscillation de l'extrémité de l'abdomen a une amplitude de 83° et dure 0,08 seconde. Une séquence de tremblement comporte en moyenne 2,4 oscillations (fig 3). Le comportement individuel provoque fréquemment la formation d'un groupe serré d'ouvrières. Lorsque 10 ouvrières au minimum se rassemblent sur le tronc près de l'entrée du nid, il se produit au sein du groupe une remarquable coordination des tremblements individuels. En général une ouvrière commence à trembler, ce qui stimule les voisines à faire de même et cette réaction se propage comme une onde dans tout le groupe. Lorsqu'un frelon *V multimaclata* arrive à l'entrée du nid, le nombre de gardiennes à la surface de l'arbre s'accroît rapidement. Au bout de 2 minutes le groupe est constitué de 20 abeilles et 5 minutes plus tard, on en a dénombré 32. Lorsque le frelon arrête son vol stationnaire et s'en va, le comportement de tremblement s'arrête et le nombre de gardiennes diminue à nouveau pour n'être plus que de deux à huit. Les ouvrières de *V multimaclata* qui chassent planent à 5 à 10 cm devant l'entrée du nid dans une position plus ou moins stationnaire et bloquent le chemin de vol direct de retour au nid. Lorsqu'une abeille s'approche pour rentrer au nid, le frelon réagit en allongeant et étendant ses pattes. Il accomplit fréquemment des retournements et des changements de position rapides face à l'abeille qui rentre (fig 5). En raison de la ressemblance évidente avec le gardien de but dans un match de football, nous proposons le terme de «comportement de gardien de but» pour cette technique de chasse particulière. Lorsque *V multimaclata* chasse, les abeilles essaient d'éviter le prédateur en se posant sur le tronc d'arbre hors de portée du frelon. Elles arrivent près du groupe de gardiennes qui tremblent et de là terminent les derniers centimètres par une course rapide. Le frelon ne réagit pas

aux abeilles lorsqu'elles sont posées. Lorsqu'il parvient à saisir une abeille qui rentre, il l'emporte jusqu'à une feuille ou une branche proches. Là il retourne avec ses pattes l'abeille bourdonnante et lui tranche la tête d'un coup de mandibule, puis s'éloigne en emportant sa proie décapitée. Au cours d'une période d'observation de 12 heures, une ouvrière de *V. multimaculata* a attrapé 14 proies. La capture a eu lieu en moyenne 6,5 minutes après l'arrivée du frelon. À la fin de l'observation nous avons amené le frelon, attaché à un fil, en contact avec un groupe d'abeilles à l'entrée du nid. Immédiatement les gardiennes l'ont emballé. Lorsque nous l'avons extrait en tirant sur le fil, 40 abeilles environ étaient accrochées au frelon (fig 6). Nous avons placé la boule d'abeilles sur la main de l'expérimentateur; la température était élevée, nettement au-dessus de 37 °C. Lorsqu'au bout de 10 minutes nous avons écarté les abeilles, le frelon était mort, comme cela a déjà été rapporté pour certaines espèces japonaises. L'analyse du tremblement d'*A. nuluensis* a révélé plusieurs similitudes avec celui d'*A. cerana* (tableau I) et le détail des mouvements d'*A. nuluensis* ressemble à des descriptions d'*A. cerana* faites antérieurement. En outre les situations biologiques correspondent : les deux espèces exécutent un tremblement à l'entrée du nid comme défense de groupe contre un frelon prédateur. Les différences proviennent du comportement prédateur hautement spécialisé de *V. multimaculata*. De façon typique, les ouvrières de *Vespa* qui chassent n'attaquent pas les abeilles en vol ; elles attrapent avec succès des abeilles sur le substratum près de l'entrée du nid. En riposte *A. cerana* a développé une défense de groupe. Dès qu'un frelon apparaît, les abeilles se déplacent ensemble et exécutent un tremblement. Ce comportement détourne les frelons. Si un frelon attaque un membre du groupe, les abeilles s'accrochent l'une à l'autre et le tuent par emballement. Ce comportement a aussi été

observé chez *A. nuluensis* lorsque le frelon a été mis en contact avec les gardiennes.

***Apis nuluensis* / comportement défensif / *Vespa* / comportement prédateur**

Zusammenfassung — Beobachtungen zur Kolonieverteidigung von *Apis nuluensis* Tingek, Koeniger und Koeniger, 1996 und das Beutefangverhalten der Hornisse *Vespa multimaculata* Perez, 1910. Das Kolonieverteidigungsverhalten von *Apis nuluensis* und das Beutefangverhalten von *Vespa multimaculata* wurden am Eingang eines natürlichen Nestes von *Apis nuluensis* beobachtet und mit Videoaufnahmen dokumentiert. In Anwesenheit von *Vespa multimaculata* zeigten Wächterbienen alle 1.01 ± 0.17 ($n = 102$) Sekunden ein Körperschüttelverhalten. Zu Beginn dieses Bewegungsmusters hebt die Biene die Spitze des Abdomens leicht an, spreizt die Flügel und exponiert die Nasonovsche Drüse. Die seitliche Auslenkung der Abdomenspitze hat eine Amplitude von 83 Grad und eine Dauer von 0,08 s. Die Schüttelbewegung enthält im Mittel 2,4 Schwingungen (Abb 3). Häufig führt individuelles Körperschütteln sehr rasch zur Bildung einer Arbeiterinnengruppe. Sobald sich 10 oder mehr Arbeiterinnen auf dem Stamm in der Nähe des Nesteingangs versammeln, kommt es zu einer bemerkenswerten Koordination des individuellen Schüttelverhaltens innerhalb der Gruppe. Meist beginnt ein einzelnes Tier mit dem Körperschütteln und veranlasst damit die benachbarten Tiere dasselbe zu tun. Diese Reaktion setzt sich in einer wellenartigen Bewegung über die ganze Gruppe fort. Sobald eine *Vespa multimaculata* auf Beutefang in der Nähe des Stockeingangs erschien, kam es zu einer raschen Zunahme der Anzahl von Wächterbienen auf der Aussenseite des Baumstamms. Nach zwei Minuten war die Gruppe auf 20 Bienen angewachsen, fünf Minuten später wurden 32 Bienen gezählt. Nach-

dem die vor dem Nesteingang schwebende Hornisse fortgeflogen war, hörte das Körperschüttelverhalten auf und die Anzahl der Wächterbienen nahm wieder auf 2 bis 8 ab. Während der Jagd auf Arbeiterinnen schwebte die *Vespa multimagulata* etwa 5 bis 10 cm vor dem Nesteingang in einer mehr oder weniger stationären Position und blockierte hierdurch den direkten Flugweg der in das Nest heimkehrenden Arbeiterinnen. Wenn die zurückkehrenden Arbeiterinnen in die Nähe der Hornisse kamen, reagierte diese durch Ausstrecken und Ausbreiten der Beine. Häufig vollführte sie schnelle Wendungen und Positionswechsel in Richtung der einfliegenden Bienen (Abb 5). Wegen der offensichtlichen Ähnlichkeit mit dem Verhalten von Tormännern schlagen wir den Namen "Torhüterverhalten" für diese Jagdtechnik der Hornisse vor. Die anfliegenden Bienen versuchten jagende *Vespa multimagulata* zu umgehen, indem sie außerhalb ihrer Reichweite auf dem Baumstamm landeten. Häufig landeten sie nahe der Gruppe körperschüttelnder Wächterbienen und bewältigten die letzten cm ihrer Heimkehr durch schnelles Rennen. Die Hornisse reagierte auf diese Bienen nach ihrer Landung nicht mehr. Gelang es der Hornisse, eine zurückkehrende Biene zu ergreifen, flog sie davon und trug die Biene zu einem nahegelegenen Blatt oder Zweig. Dort drehte sie die summende Biene mit ihren Beinen um und biss ihr den Kopf ab. Danach flog sie mit der kopflosen Beute davon. Während einer Beobachtungsdauer von insgesamt 12 h hatte eine *Vespa multimagulata* 14 erfolgreiche Fänge. Im Mittel war die Hornisse etwa 6.5 Minuten vor dem Fang der Beute erschienen. Zu Ende der Beobachtung brachten wir die Hornisse an einem Draht befestigt mit der Bienengruppe am Nesteingang in Kontakt. Die Wächterinnen knäulten die Hornisse sofort ein. Als wir den Draht zurückzogen, klammerten sich etwa 40 Bienen an der Hornisse fest (Abb 6). Wir legten den Bienenknäuel auf Nk's Hand. Seine

Temperatur war sehr hoch, deutlich über 37 °C. Wie über einige Japanische Arten von *Vespa* berichtet, war auch *Vespa multimagulata* tot, als wir die Bienen nach insgesamt 30 min entfernten. Die Untersuchung des Körperschüttelverhaltens von *Apis nuluensis* zeigte einige Ähnlichkeiten mit dem von *Apis cerana* (Tabelle I), und die Einzelheiten der Bewegung von *Apis nuluensis* waren den früher von *Apis cerana* beschriebenen ähnlich. Weiter entsprachen sich auch die biologischen Situationen: bei beiden *Apis* - Arten tritt das Körperschüttelverhalten am Nesteingang als Gruppenverteidigungsverhalten gegen räuberische Hornissen auf. Unterschiede gab es allerdings durch das hochspezialisierte Beutefangverhalten von *Vespa multimagulata*. Üblicherweise greifen räuberische Arbeiterinnen von *Vespa* keine fliegenden Bienen an. Sie können dagegen erfolgreich einzelne Arbeiterinnen vom Untergrund nahe des Nesteingangs aufgreifen, wogegen *Apis cerana* als Gegenstrategie ein Gruppenverteidigungsverhalten entwickelt hat. Sobald eine *Vespa* erscheint, rücken die Bienen zusammen und führen das Körperschüttelverhalten aus. Hierdurch wehren sie die Hornissen ab. Falls eine Hornisse eine Bienengruppe angreift, klammern sich die Bienen zusammen und töten die Hornisse durch Einknäulen. Das Experiment mit der an einem Draht gehaltenen Hornisse legt nahe, dass dieses Verhalten auch von *Apis nuluensis* gezeigt wird.

***Apis nuluensis* / Verteidigungsverhalten / *Vespa* / Beutefangverhalten**

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