

## Have native Hymenoptera or Africanized bees become aggressive foragers due to resource competition?

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### ABSTRACT

We observed and ranked foraging behavior among competing hymenopterans. Africanized honeybees, observed in Yucatan, Mexico attacking *Trigona fulviventris* (Meliponini) on flowers in 2005, were again studied there in 2015 and 2016. We used honey-water (of *Apis* or *Melipona*) and standardized baiting to observe bee and wasp foraging. Of the recorded 7578 aggressive interactions, nearly 2/3 were intraspecific. Africanized *Apis mellifera* rarely displayed even mild aggressive behavior toward Meliponini, including *T. fulviventris*. Similarly, previous work documented no agonism by *Cephalotrigona*, but it attacked *Melipona beecheii* and *Apis* in our study. Individual, flexible behavior is thereby implicated in foraging behavior. The common *T. fulviventris* was persistently aggressive against *Apis*, while *Melipona*, the largest native bee and of *Apis* size, showed no aggression toward other insects; it seldom foraged honey water presented as bait. Among the 1047 interactions between *Apis* and 10 native species, 44 included aggression by *Apis*, often against large polistine wasps. *Apis*, *Cephalotrigona* and *Trigona* were intensively intraspecifically aggressive, *Trigona*, *Cephalotrigona*, *Frieseomelitta*, *Nannotrigona*, *Plebeia* and Epiponini often attacked other species, and *Apis* was the most widely attacked species and frequently displayed evasive behavior, which may suggest evolution has yet to mold interactions between invasive Old World *Apis* and native Neotropical insects.

**KEYWORDS:** *Apis*, epiponine wasps, Meliponini, foraging evolution, aggressive interactions, resource competition

### INTRODUCTION

A study in the Yucatan peninsula of Mexico reports aggressiveness by foraging honeybees toward a native stingless bee (Meliponini), *Trigona fulviventris* [1]. Because such behavior had not been reported at any natural or controlled experimental setting for this colonizing bee, since its spread from Brazil in 1956, it was suggested that exotic Africanized honeybees had evolved aggressive foraging behavior [1]. Three “attack” observations were recorded, but a tabulation of interactions involving *A. mellifera* was lacking. We therefore studied, in the same area, bee and wasp interactions at honey-water feeders.

Agonistic encounters between organisms involve escape, aggression and defense, which for social insects occur within the colonial nest and also in the environment. The *Apis* or honeybees, the stingless honey bees (Meliponini), and other nectar feeding insects, such as wasps, flies and ants gather nutritional or building resources such as resin, fruit, Hemiptera secretions, animal leavings, and flower products, during the collection of which they may interact aggressively to some degree [2-10]. Furthermore, aggressive defensive behavior at colonial nests is often positively correlated with aggression over resources [11-13]. To experimentally study foraging behavior, artificial feeders are often used, but feeders must be properly designed to not crowd foragers together or present an uncommonly large resource, which may resemble

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that at the nest itself [13-19]. Agonism is presumably expressed due to a combination of olfactory, tactile and visual stimuli [20]. Water was, however, an additional site at which attack behavior by *Apis* was observed in the earlier study [1]. In the present paper, we are only interested in competitive behavior at food or building material resource sites. There is, nonetheless, some merit in discussing possible learned behavior at water sites, which is taken up further in the 'CONCLUSION', while briefly clarified here. Honeybees collect water to cool their nest; stingless bees collect mud at wet sites, and both wasps and Meliponini collect water for non-cooling purposes [7, 11, 13]. In foraging settings where colonial bees come into contact, if they are conspecific but not of the same colony they often fight, lunge, bite or grapple. This would occur at a trough of water, a trough or pool of honey or sugary liquids, ripe fruit, or anywhere there is prolonged contact with other foragers. Such pool resources differ significantly from a series of small 'point resources' like those presented in flowers. We avoided the 'resource pool fallacy' by using artificial feeders that distribute the resource quite evenly but in very small parcels, similar to individual

flowers (Fig. 1). More stationary feeding, like foraging at a resin source on a tree, or honey at a hymenopteran nest, readily leads to fighting. Feeders that we designed encouraged forager movement. If aggressive behavior while on flowers is naturally expressed, it should be evident at an experimental feeder where rewarding resource is obtained and foragers are in visual, tactile and olfactory contact.

Several kinds of behavior can occur among foragers at artificial feeders and natural resources. For example, threat (rushing or threatening 'posture'), attack (biting), displacement and killing (by biting) were observed in all four of the *Trigona*, among 16 species of Meliponini studied by Johnson and Hubbell [2, 3, 14] at both natural and artificial resources in Pacific Costa Rica (see also [10]). Half of the species never foraged with competitors using an aggressive behavior. However, a few routinely used intraspecific or interspecific threatening, typified by rushing at a competitor, with wings partly spread in a "V-wing display". The 16 native Costa Rican stingless bee species included *Melipona*, *Tetragona*, *Cephalotrigona*, *Plebeia*, *Nannotrigona*, *Scaptotrigona*, *Trigona*, *Trigonisca*,



**Fig. 1.** Native stingless bees (Meliponini-*Nannotrigona*, *Plebeia*, *Partamona*), Africanized honeybees (*Apis mellifera*) and wasps (Polistinae) visiting section of a fiber hat 'feeder' in Quintana Roo, Yucatan Peninsula, Mexico (Photo by D. W. Roubik).

*Tetragonisca*, *Scaura* and *Partamona*. Most genera, and the same species, were studied in the present work, and we categorized behavioral interactions in a way similar to previous authors.

## MATERIALS AND METHODS

The study area, Sian Ka'an Biosphere Reserve, in the southeastern Yucatan peninsula, comprises 500,000 ha. Its surrounding buffer zone is also forested, and centered approximately at 19°43' N, 87°48' W. Most of the study was within the reserve and its buffer zone during 20-28 June, 2015 while 7 days of study during 4-12 August were made at the forested campus and meliponary at Ecosur, in Chetumal, Quintana Roo. In addition, baiting studies were performed during September, 2016, at Ecosur. The median annual temperature is approximately 28 °C, with a mean of 29-30 °C during the study months (state meteorological records, Quintana Roo). There were 50 experimental sites within a 12 km transect of forest in Sian Ka'an and its access road (within four km at the beginning and four km at the end of the transect), one within the town of Felipe Carrillo, and six at the Ecosur campus in Chetumal. Small apiaries were near two of the 8 areas in Sian Ka'an, thereby increasing the chances of encounter between the honeybee and native Hymenoptera. A meliponary at the Ecosur campus, which contained hives of *Melipona beecheii* and *Cephalotrigona zexmeniae*, was employed specifically to study foraging by those species. The business site of Mr. Daniel Pech, in Felipe Carrillo Puerto, Quintana Roo, was used to study *Apis* and *Nannotrigona*.

In the Sian Ka'an Biosphere area, a 12 km transect along the narrow access road through forest was used to set up honey-water feeders. The advantage of studying bee foraging with sugar or honey resources at feeders is that the setting of forager interaction, along with resource quality and quantity, can be standardized, and observations replicated at different sites. The honey of local Africanized *Apis mellifera*, which has approximately 80% sugar content, was diluted to approximately 40% sugar and sprayed (ca. 12 ml total) using a hand-held sprayer to make a baiting site, with fine to medium-coarse spray. If bees or wasps arrived at the sprayed leaves, a segment of "fiber hat" was hung on a branch (Fig. 1). The 'hat feeder' was

used to quantify the number of aggressive acts of each species, and to observe behavioral details. We watched foragers on leaves, attracted by a fine spray of honey-water, to make further observations of interactions. The solution was replenished with several medium-fine sprays when diminished by forager activity, usually each 5 to 10 min. For a second study at Ecosur Campus, the honey of *Melipona beecheii* was diluted to 40% sugar (honey ca. 70% sugar content) and then applied both to vegetation and hat segments, with a sprayer. At the same time, a 50/50 mix of *Apis* and *Melipona* honey, diluted to 40% total dissolved sugar by weight, was sprayed in the nest entrance of 20 *Melipona* hives at our meliponary. After ½ hour, one bee arrived at each of two honey-water areas, and this is the only record we took of *M. beecheii* in 2015. However, in September, 2016, one colony responded with recruitment to honey-water of *Apis* that was slightly fermented, and behavioral bioassays at the hat segment feeders took place.

The different sites with honey-water numbered 57, where *Apis* foraged a total of 23 site-days. Honey-water initially applied at 10 sites rapidly attracted foraging bees and other insects. Almost all sites received visits from native Hymenoptera. There were few occurrences of massive recruitment, whereby hundreds of foragers of a single species arrived (see DISCUSSION). Four observers recorded behavior, simultaneously, at separate sites. The studies at each site continued for two, seven and nine days at Felipe Carrillo, Chetumal and Sian Ka'an, respectively. Each day, unless interrupted by rain, observations took place for at least one hour, with detailed notes each five to 10 min, for up to four hours.

We photographed and made videos of forager interactions. The noted interactions included all of the forms of contact or above-mentioned "V-wing" threat, but did not include the mere landing on another forager, which did not appear to be an aggressive act. The species and number of bees and/or wasps coming to the feeders and leaves on which bait was sprayed were sometimes estimated. A sampling of 6 site-days by the first author, in 2015, noted an average number of 5 to 50 of a given species at a baiting site. In 2016, during two hours of foraging by *Melipona* and *Apis* at the same bait near the Ecosur meliponary, up to 40 *Melipona* and up to 20 *Apis* were foraging on the

experimental feeder, with a mean of approximately 8 foragers each. Microscopic examinations were made to determine *Plebeia* and *Trigonisca* spp., while others were identified to species on sight alone. The wasps, however, were identified to genus or combined, and in the field, not all observers could distinguish different species of *Plebeia*, which were combined in analyses.

## RESULTS

The total observed interactions involving attacks, ranging from biting to chasing, included 7578 behavioral acts (Tables 1 and 2). Native foragers (with the exception of polistine wasps) and *Apis* attacked conspecifics of other colonies (Table 1). A few of the native species were studied rarely, including *Trigona fuscipennis*, *Partamona orizabaensis*, *Trigonisca* and *Nannotrigona testaceicornis*, but each had some interaction with *Apis*, and were mildly attacked by it in a few instances. Of the 1047 interactions between *Apis* and 10 native species, only 44 included aggression by *Apis*, often against large polistine wasps. A ranking

of foragers by their tendency to attack others not of their species (Table 1) shows that *Apis* was less aggressive than other insects, by a factor of roughly 2x to 15x, on an average basis, summarized from 10 to 46 site-days (Table 1). For actual encounters between *Apis* and native foragers (Table 2), the wasps were equal to honeybees in their aggression toward the invasive bee, while native bees were usually 50-100 times more aggressive toward the honeybee than that species was toward them. *Melipona beecheii* was unique in displaying no aggressive foraging behavior toward other species, but *Apis* was quite similar, and *Melipona* only visited a feeder once in the study.

*Apis mellifera* was less likely to attack a forager not of its own species or taxonomic group than were all native foragers that were repeatedly observed. For interactions with *A. mellifera*, those with *T. fulviventris* were noteworthy because *Apis* fled and rapidly flew to other feeding places, clearly demonstrating avoidance of *T. fulviventris*. Eight species often interacted aggressively with *A. mellifera*, but others were seen too infrequently

**Table 1.** Observation summary. \*N attacks by listed taxa, species given in text; *Plebeia* and Polistinae are of >1 species. \*\*Mean of total interspecific attacks per site-day.

Taxa*	N total interactions	N Intraspecific attacks	N Interspecific attacks*	Total site days	Intraspecific attack site days	Mean interspecific aggression per site-day**
<i>Apis mellifera</i>	1227	131	44	23	8	2.5
<i>Cephalotrigona</i>	2016	744	1272	39	12	39.8
<i>Trigona</i>	469	227	242	40	12	4.9
<i>Plebeia</i>	1578	440	1138	46	16	9.3
<i>Frieseomelitta</i>	1661	456	1205	28	7	35.7
Polistinae	387	0	387	10	0	10.9

**Table 2.** Interspecific aggression records and victim index, related to interaction with *Apis*. Ratios of interspecific attacks by each native Hymenoptera group (Other) are compared to *Apis*.

	<i>Apis</i>	Other	Victim index
Polistinae	24	22	1.09
<i>Partamona</i>	7	16	0.44
<i>Plebeia</i>	1	81	0.01
<i>Trigona</i>	3	192	0.02
<i>Cephalotrigona</i>	8	468	0.02

to establish interaction tendencies with either exotic or native foragers. The aforementioned species were *Cephalotrigona zexmeniae*, *Trigona fulviventris*, *Frieseomelitta nigra*, *Plebeia* (2 spp.), *Polybia* sp., *Agelaia* sp. and *Synoecca* sp. The species with too few observations to generalize upon were *Trigonisca maya*, *Partamona orizabaensis*, *Nannotrigona perilampoides*, *Melipona beecheii* and *Trigona fuscipennis*.

Threat interactions, as opposed to physical contact or biting, were usually part of a brief attack, rushing, lunging, nipping or similar behavior, while forewings were extended in a “V” position over the abdomen. Pure threat, with no physical contact, was most noticeable in *Apis* and *Nannotrigona*. *Nannotrigona perilampoides* employed a V-wing stance during much of its foraging while at feeders.

In our study, *Trigona* and *Plebeia* were frequently attacked, *Apis* and *Cephalotrigona* were more frequently attacked, and *Frieseomelitta* and the polistines (*Polybia*, *Agelaia* and *Synoecca*) were substantially (ca. 30-50%) less often attacked, in the species combinations we observed. Aggressiveness was displayed most often by *Trigona*, *Cephalotrigona* and *Frieseomelitta*, somewhat frequently among *Plebeia*, and least by honeybees and polistines. In interspecific aggression among native foragers, *Trigona fulviventris* attacked *Plebeia*, polistines, *Partamona*, *Trigona fuscipennis* and *Apis*. *Plebeia* attacked polistines, *Frieseomelitta*, *Cephalotrigona*, *Trigona* and *Partamona*. *Cephalotrigona* attacked *Melipona*, *Plebeia*, *Nannotrigona*, *Frieseomelitta* and polistines. *Frieseomelitta* attacked *Plebeia*, *Cephalotrigona* and polistines. *Polybia* was observed attacking *Plebeia*, *Frieseomelitta* and *Trigona*. The few observations of interspecific interactions preclude summarizing interactions of the other forager species.

The record of *Cephalotrigona zexmeniae*, *Partamona orizabaensis*, *Frieseomelitta nigra*, and *Plebeia* spp. fighting with conspecifics and other species has not to our knowledge been previously noted, as were observations of *A. mellifera* attacking Epiponini. The polistine wasps did not fight among themselves, which perhaps is related to their very limited recruitment, or other factors that are unknown. These foragers included, but were probably not limited to, *Polybia*, *Synoecca* and *Agelaia* in our studies.

## DISCUSSION

One individual usually corresponded to one recorded behavioral act. However, when *T. fulviventris* hovered and then darted at other foragers, the same individuals, both victim and aggressor, could be scored during successive attacks. Thus, if one bee repeatedly darted at another, each act was counted. This also was true for *Cephalotrigona*, which did not hover, but walked over the feeder and attacked a series of foragers. This degree of “pseudoreplication” might pose a problem for interpretation, unless multiple sites and temporal replication were incorporated in the study. Because our work had 10-46 site-day replications for foragers, over two years and three sites, we believe the insights gathered are sufficient, at least, to answer the question: Do they fight at natural resources and can we predict such behavior?

When a social insect colony elects to forage massively on a single resource patch, it may recruit 100s to 1000s of nest mates in a short time [15, 20-22]. That kind of recruitment may displace a competitor, whether or not either competitor is aggressive. In the present study, we found a behavior in *Trigona* and its allied genera *Cephalotrigona* and *Frieseomelitta* that seems to allow aggressive displacement. In the experimental setting, we witnessed a massive arrival of *Partamona*, *Frieseomelitta* and *Trigona* on a few occasions, but the former was only mildly aggressive toward other foragers. Similarly, *Plebeia* often recruited rather heavily, but not rapidly or in large numbers, and was less aggressive. It did, however, display marked aggression toward colonizing *Apis*. Our work, because it employed a relatively small resource in a comparatively small patch, might therefore not serve as an indication of competitive prowess or probability of success. We suggest that it does highlight the principal reason for making the study, to ascertain whether a unique foraging behavior had evolved in an immigrant, honeybee species, new to the continent.

Thus, honeybees from Africa have not evolved aggressive foraging behavior since their colonization, hybridization with naturalized or kept *Apis mellifera* of temperate origin, and wide dispersal in tropical America since the late 1950s, and Mexico since the 1990s [23, 24]. They do, however, seem to display the same kind of flexibility that we

found among native *Cephalotrigona* and *Partamona*, which had heretofore been studied in Costa Rica, but revealed no predictable aggressive foraging behavior [2, 3, 14]. The suggestion can be made that individual foragers learn from foraging experience and, if they are repeatedly attacked by a given species, can be conditioned to display agonism in a certain context.

A general theory developed to explain foraging bee competition at natural resources and at sugar solution feeders posits that aggressive species dominate rich resource patches, or dense floral displays, by arriving there in groups [2,3 10, 21]. Most bees and other flower visitors practice scramble competition and resource partitioning [23], with no overt aggressive mechanisms. At a large resource which elicits recruitment behavior of social insect colonies, e.g. flowering tree canopies in tropical forests, and at sugar-water bait or honey-water, foraging units of roughly 50-200 workers, and from the largest colonies of *Trigona*, thousands of workers [22], compete aggressively with conspecific groups. One usually displaces the other, although if evenly matched in number, substantial mortality may occur during contests between rival groups [2, 3].

Foraging behavior of colonial bees is influenced by body size, recruitment performance-thus group and colony size-and “weapons” such as toothed mandibles [10, 12]. Accordingly, one would predict aggressive foraging for *Trigona* and also *Cephalotrigona*, with 1-5 pronounced mandibular teeth which other Meliponini lack [6, 13, 15]. As Johnson reasoned, *Trigona*, with large colonies and group arrival at forage, may benefit from aggressive foraging by monopolizing a resource patch of high quality, rather than seek small or scattered resources.

*Trigona* may be more likely than honeybees to be aggressive, because the latter can forage over an extremely large area (20,000 ha for *A. mellifera* [13]) and while having no mandibular denticles to augment their bite, they have a sting, but its use ends their life. They are ill-equipped to skirmish except by biting, rushing, threatening with an open-wing “V” or briefly contacting a rival forager. Although the biting behavior between *Apis* of different colonies was noteworthy, this behavior seems more typical of nest defense than of foraging

while on flowers. It is open to speculation that diluting *Apis* honey to mimic floral resources also influences the intensity of *Apis* reactions in a particular foraging context. It may elicit behavior usually restricted to intraspecific nest robbing [13].

Their extraordinary communication and recruitment abilities grant honeybees flexibility. They gain little from sacrificing workers in battles. In other studies they displayed no fighting with highly aggressive *Trigona williana* and *T. branneri*. Those species persistently attacked honeybees, but eventually gave up the honey-water feeders [15].

## CONCLUSION

A honeybee forager of the Africanized, Western hive bee *Apis mellifera*, in the Americas, attacking another bee ‘out of the blue’ is probably a learned behavior and not a newly evolved foraging tactic. The population of this invasive bee variety has had 60 years of practice with >30 potentially aggressive *Trigona*, and has yet to show behavior other than scramble competition, evasive escape behavior while under attack, and intensive foraging and flight activity. Its only notable aggression was intraspecific (Fig. 2), but on rare occasions under crowding during feeding, it lunged at, but did not bite, native species. Foraging at other resources, including water [1], revealed aggression of wasps toward *Apis*. In addition, certain pesticide chemicals or behavior-altering compounds contained in flowering plants [e.g. 25] may occasionally evoke unusual behavior in bees. The first author observed such behavior in Africanized honeybees foraging at *Brugmansia*, a night-blooming solanaceous plant with alkaloids in its nectar, which continues to be taken by bees during the day. The honeybees rapidly flew at other foragers around the flowers.

It would be interesting to study whether some of the native species now recognize and instinctively attack *Apis mellifera* while visiting flowers. Because they would have much to lose to the highly effective foraging colony, there is some reason to believe natural selection would adjust foraging behavior and associated physiology or biochemistry (see [8]). Furthermore, the unusually high rate of attack on honeybees by native species, at least in foraging assays we employed, may later be replaced with chemically or visually mediated, less costly, interspecific behavior. In summary,



**Fig. 2.** Honey-water feeder with *Trigona fulviventris* about to attack *Apis mellifera*, both honeybees display the “V-wing” (see text); two *A. mellifera* biting another worker. Quintana Roo, Yucatan Peninsula, Mexico. Photos by D. W. Roubik.

the fact that *Apis mellifera* has had a tiny period of contact with native species, relative to the millions of years in which those have been interacting, suggests there is no reason now to expect corresponding genetic population changes that have altered the behavior of honeybees or their competitors. Their behavior should reflect stimuli and responses from different continents.

#### CONFLICT OF INTEREST STATEMENT

The authors report they have no conflict of interest for the present work.

#### REFERENCES

- Cairns, C. E., Villanueva-Gutiérrez, R., Koptur, S. and Bray, D. B. 2005, *Biotropica*, 37, 686.
- Johnson, L. K. 1974, The Role of Agonistic Behavior in the Foraging Strategies of *Trigona* bees. Ph.D. Thesis, Univ. California, Berkeley.
- Johnson, L. K. and Hubbell, S. P. 1974, *Ecology*, 55, 120.
- Roubik, D. W. 1978, *Science*, 201, 1030.
- Roubik, D. W. 1979, Proc. V<sup>th</sup> Intl. Symp. Pollination, D. Caron (Ed.), Maryland Agri. Exp. Sta. Misc. Pub. No. 1, College Park, Maryland, 403.
- Roubik, D. W. 1981, *Rev. biol. Trop.*, 29, 177.
- Richter, M. R. 2000, *Ann. Rev. Entomol.*, 45, 121.
- Peso, M., Elgar, M. A. and Baron A. B. 2015, *Biol. Rev.*, 90(2), 542-59. doi: 10.1111/brv.12123.
- Roubik, D. W. 1996, The Conservation of Bees, A. Matheson, S. L. Buchmann, C. O’Toole, P. Westrich and I. H. Williams (Eds.), Academic Press, Ltd., London, 173.
- Hrcir, M. and Maia-Silva, M. 2013, Stingless bees process honey and pollen in cerumen pots. P. Vit and D. W. Roubik (Eds.), Facultad de Farmacia y Bioanálisis, Universidad de Los Andes; Mérida, Venezuela, 1. (<http://www.saber.ula.ve/handle/123456789/35292>)
- Roubik, D. W. 2006, *Apidologie*, 37, 124.
- Shackleton, K., Al Toufailia, H., Balfour, N. J., Nascimento, F. S., Alves, D. A. and Ratnieks, F. L. W. 2015, *Behav. Ecol. Sociobiol.*, 69, 273.
- Roubik, D. W. 1989, *Ecology and Natural History of Tropical Bees*, Cambridge, New York.
- Hubbell, S. P. and Johnson, L. K. 1978, *Ecology*, 59, 1123.
- Roubik, D. W. 1980, *Ecology*, 61, 836.
- Roubik, D. W. 1996, *Tropical Rainforest Research: Current Issues*, D. Edwards, W. E. Booth and M. Choy (Eds.), Kluwer Acad. Publ., Dordrecht, 59.
- Roubik, D. W. 1999, *J. Kansas Entomol. Soc.*, 72, 394.
- Roubik, D. W., Inoue, T. and Hamid, A. 1995, *Tropics*, 5, 81.

19. Roubik, D. W., Inoue, T., Hamid, A. and Harrison, R. 1999, *J. Kansas Entomol. Soc.*, 72, 256.
20. Buchwald, R. and Breed, M. D. 2005, *Animal Behaviour*, 70, 1331.
21. Roubik, D. W. 2002, *Proc. Symp. "Modelling and experimental research on genetic processes in tropical and temperate forests"*, B. Degen, M. Loveless and A. Kremer (Eds.), *Documentos de Embrapa Amazonia Oriental*, Belém, 30.
22. Roubik, D. W. 2017, *Pot-Pollen in Stingless Bee Melittology*, P. Vit, S. R. M. Pedro and D. W. Roubik (Eds.), Springer Nature, New York, 67.
23. Roubik, D. W. 2009, *Acta biol. Colombiana*, 14, 115.
24. Villanueva-Gutiérrez, R., Roubik, D. W. and Porter-Bolland, L. 2015, *Bee-plant interactions: Competition and phenology of flowers visited by bees*. In: *Biodiversity and conservation of the Yucatán Peninsula* (G. A. Islebe, S. Calmé, J. L. León Cortéz and B. Schmook (Eds.)), Springer International Publishing Switzerland, 131.
25. Yang, E. C., Chuang, Y. C., Chen, Y. L. and Chang, L. H. 2008, *J. Econ. Entomol.*, 101, 1743.