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# Host Location by Ichneumonid Parasitoids is Associated with Nest Dimensions of the Host Bee Species

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## Keywords

*Grotea*, *Labena*, host finding, vibrational sounding

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## Abstract

Parasitoid fitness depends on the ability of females to locate a host. In some species of Ichneumonoidea, female parasitoids detect potential hosts through vibratory cues emanating from them or through vibrational sounding produced by antennal tapping on the substrate. In this study, we (1) describe host location behaviors in *Grotea gayi* Spinola (Hymenoptera: Ichneumonidae) and *Labena* sp. on nests of *Manuelia postica* Spinola (Hymenoptera: Apidae), (2) compare nest dimensions between parasitized and unparasitized nests, (3) correlate the length of *M. postica* nests with the number of immature individuals developing, and (4) establish the relative proportion of parasitized nests along the breeding period of *M. postica*. Based on our results, we propose that these parasitoids use vibrational sounding as a host location mechanism and that they are able to assess host nest dimensions and choose those which may provide them with a higher fitness. Finally, we discuss an ancestral host–parasitoid relationship between *Manuelia* and ichneumonid species.

## Introduction

Larvae of parasitic Hymenoptera feed on a single host individual and either prevent it from growing beyond the stage when parasitization occurred (idiobiont parasitoids) or allow the host to remain mobile and continue to grow (koinobiont parasitoids; Askew & Shaw 1986). In both larval lifestyles, the fitness of the parasitoid depends on the ability of the parasitoid female to find its host (Djemai *et al* 2004). Some species of Ichneumonoidea parasitize hosts which are deeply concealed within a substrate (e.g., wood, plant stems, rolled leaves or buds; Gauld 1988). Host location by female parasitoid can be achieved by exploiting chemical (Xiaoyi & Zhongqi 2008, Cusumano *et al* 2010, González *et al* 2011) or vibratory cues emanating from the host (Meyhöfer & Casas 1999, Joyce *et al* 2011) or by means of vibrational sounding, a form of echolocation consisting of tapping the substrate with the tips of the antennae and detecting the reflected echoes with the subgenual organs in the legs (Broad & Quicke 2000).

Vibrational sounding and transmission of vibrations are affected by environmental conditions of host microhabitats

such as temperature (Samietz *et al* 2006), by physical properties of the substrate in which hosts are developing such as hardness and density (Fischer *et al* 2003), and depth within the substrate at which the host is located relative to the size of the female parasitoid (Xiaoyi & Zhongqi 2008), as well as by the size of the parasitoid female (Otten *et al* 2001). In addition, the vibration produced by the female parasitoid may be reflected differentially by solid and hollow substrates (Vilhelmsen *et al* 2001). However, although parasitoid females use vibrational cues to discriminate between hollow and solid sections of substrates (Wäckers *et al* 1998), the effect of cavity dimensions on the selection of potential oviposition places has not been evaluated.

The genus *Grotea* (Hymenoptera: Ichneumonidae) [synonym: *Macrogrotea* (Gauld & Wahl 2000)] has been reported to parasitize *Chilicola venticola* Packer (Hymenoptera: Colletidae) (Packer 2004), *Chilicola deborahae* González & Giraldo (González & Giraldo 2009), *Manuelia gayi* Spinola (Hymenoptera: Apidae) (Janvier 1933), *Manuelia postica* (Flores-Prado *et al* 2008),

*Ceratina* spp. (Hymenoptera: Apidae) (Daly *et al* 1967, Gauld 2000), and has been observed in nests of *Manuelia gayatina* Spinola (Hymenoptera: Apidae; Flores-Prado, unpublished observations), all of which are bee species that construct their nests inside stems or twigs. Furthermore, the genus *Labena* (Hymenoptera: Ichneumonidae) has been observed parasitizing *M. postica* (Flores-Prado, unpublished data). Therefore, both *Grotea* and *Labena* need to detect concealed and immobile bee hosts.

In this paper, host location behaviors of *G. gayi* and *Labena* sp. are described and factors such as nest dimension and occupancy which affect the final oviposition decision of the parasitoids examined. The results suggest the use of vibrational sounding by both parasitoid species as a mechanism for host location and the capacity of parasitoids to assess the dimensions of the nests and choose those which may provide them with a higher fitness.

## Material and Methods

### Field observations and collection of nests

Field observations were performed and bee nests collected at Altos de Lircay National Park, east of Talca, Chile (35°29' S; 70°58' W), from November 2008 until April 2009. Host searching behaviors by *M. gayi* ( $n=6$ ) and *Labena* sp. (an undetermined species;  $n=7$ ) were observed on stems of *Chusquea quila* (Poaceae: Bambuseae), a plant species used as nesting substrate by *M. postica* (Flores-Prado *et al* 2008). Nests consist of a tunnel where a *M. postica* female sequentially constructs a series of linearly arranged cells in each of which eggs are deposited (Fig 1a). Adults emerge from late summer to autumn, break cell partitions, and remain inside the tunnel as a hibernating assemblage until spring (Flores-Prado *et al* 2008).

One hundred sixty nests of *M. postica* inside *C. quila* stems were collected during each of the three following periods: November–December 2008, January–February 2009, and March–April 2009. Nest entrances were blocked with Teflon tape affixed with masking tape prior to collection; nests were transported to the laboratory in Santiago and dissected in order to observe: (1) the number of immature individuals of *M. postica* in nests collected during November–December 2008 and January–February 2009, (2) the number of newly emerged imagoes of *M. postica* in nests collected during March–April 2009, (3) the presence or absence of immature individuals (larvae or pupae) of ichneumonid parasitoids in nests collected in the three periods. Some parasitoids that survived to imago stage ( $n=6$ ) were identified as *G. gayi* ( $n=2$ ) or *Labena* sp. ( $n=4$ ). Identification was made: (1) following a specific taxonomic key for the Ichneumonidae genera of South America (Porter 1998), and

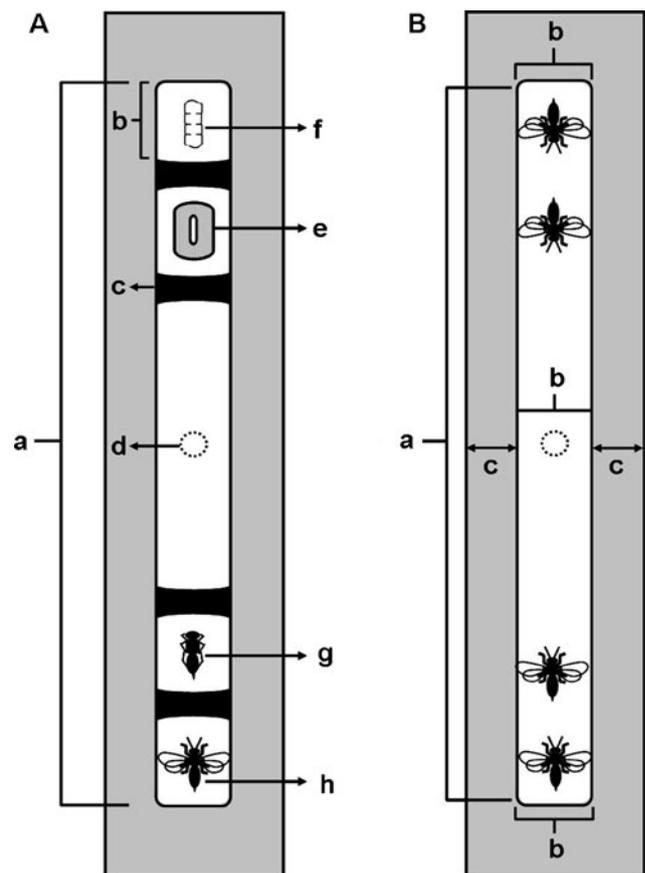


Fig 1 Diagrammatic representation of a nest of *Manuelia postica* showing the parameters measured. **a** A nest exhibiting developing individuals, as can be found before the hibernating assemblage stage. Letters refer to: *a* the tunnel, *b* a cell, *c* a partition, *d* the nest entrance, *e* an egg on a food mass, *f* a larva, *g* a pupa, and *h* a newly emerged adult. **b** A nest containing a hibernating assemblage constituted by four bees, in which the following parameters were determined: *a* nest length, *b* nest diameter, represented by the mean calculated from measures obtained at the ends of the tunnel and at the nest entrance hole, and *c* thickness of the nest wall, calculated as the mean thickness of walls on both sides of the tunnel at the nest entrance hole.

(2) through comparisons with specimens kept in the collection at the “Instituto de Entomología, Universidad Metropolitana de Ciencias de la Educación, Chile”. In order to compare nest characteristics between parasitized (i.e., at least one of the bees inside the nest is parasitized) and unparasitized nests, only nests collected in March–April 2009 were used because only during this period nest construction can be considered completed (Flores-Prado *et al* 2008). In 25 parasitized nests, nest length, mean nest diameter, and mean thickness of the nest wall were determined (Fig 1b). The dimensions described above were also registered in another set of 25 randomly chosen unparasitized nests collected in March–April 2009. Moreover, in 80 unparasitized nests of the 160 nests collected in March–April 2009, nest length and number of individuals inside nests were determined (Fig 1b).

### Data analysis

In order to explore the multivariate differences between the dimensions of parasitized and unparasitized nests (length, diameter, and wall thickness), a multivariate analysis of variance analyses was performed because all variables showed normal distribution and homocedasticity. Thereafter, individual variables were compared using Tukey's post hoc tests. The association between the length of nests and the number of individuals inside them was assessed by means of a Spearman correlation because the number of individuals did not exhibit a normal distribution. The relative proportion of parasitized nests was compared during the three collection periods using the  $Z$  test for proportions.

## Results

### Field observations

The description of host searching behaviors was based on observations of six individuals of *G. gayi* and seven of *Labena* sp. These observations were made from November 2008 until April 2009, from 0900 to 1800 hours, and represent the result of 24 days of sampling. Thus, host-searching activities show a rather low frequency. Behaviors involved in host location were similar in both parasitoid species. The nests of *M. postica* exhibit a conspicuous entrance hole (2.9 mm mean diameter; Flores-Prado *et al* 2008). The search of potential hosts by *G. gayi* and *Labena* sp. involved a hovering flight near such entrance holes. Independent of whether or not a guard female of *M. postica* was present at the nest entrance, the parasitoid landed on the substrate and walked up and down while continuously tapping the surface of the substrate with the tips of the antennae. At a certain point in time, presumably when the insect found the nest of its host, it stopped walking, repeatedly moved the ovipositor up and down, curved the abdomen, and finally inserted the ovipositor into substrate. Similar observations have been reported by Janvier (1933) in *G. gayi*.

### Data analysis

Significant differences between parasitized and unparasitized nests occurred in length, diameter, and wall thickness ( $F_{3,46}=18.94$ ,  $P<0.001$ ). The length and diameter of parasitized nests were greater than those of unparasitized nests, and the nest wall was thinner in parasitized nests than in unparasitized nests ( $P<0.01$  in the three comparisons; Fig 2).

The length of *M. postica* nests (the length of the tunnels where immature individuals are growing) and the number of individuals developing inside them were positively

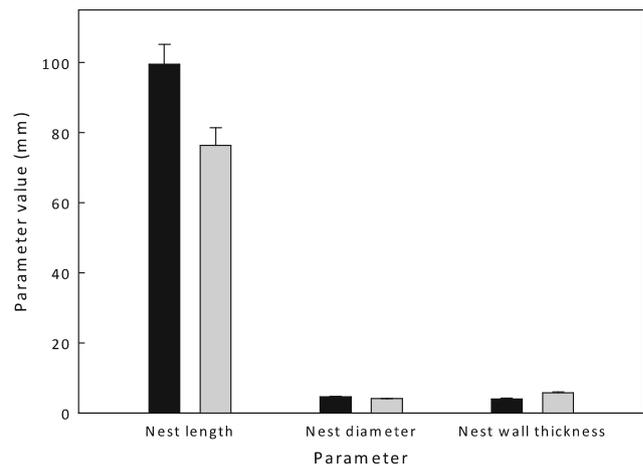


Fig 2 Dimensions of parasitized (black bars) and unparasitized (gray bars) nests of *Manuelia postica* collected during March–April 2009. Twenty-five nests of each category were examined. Different letters indicate significant differences in each of the parameters measured ( $P<0.01$ ).

correlated ( $r=0.53$ ,  $P<0.001$ ) (Fig 3). Thus, larger *M. postica* nests bear more potential hosts for ichneumonid parasitoids.

Of the 160 nests collected for each period, eight nests (5%) were found parasitized in the first period (November–December 2008), 15 (9.4%) in the second period (January–February 2009), and 46 (28.8%) in the third period (March–April 2009). The relative proportion of parasitized nests in the third period was higher than in the first ( $Z=-5.71$ ,  $P<0.05$ ) and second ( $Z=-4.45$ ,  $P<0.05$ ) periods.

## Discussion

Vibrational sounding as a mechanism of host searching is characterized by highly active behavioral displays when

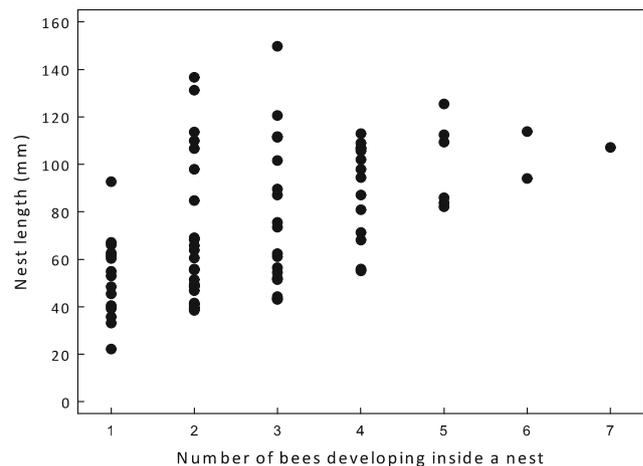


Fig 3 Correlation of nest length and number of individuals found within them. Eighty nests of *Manuelia postica* collected during March–April 2009 were examined.

females are searching for a suitable oviposition site, i.e., running up and down the stem while vigorously tapping the substrate with the antennae (Broad & Quicke 2000). The antennal tapping displayed during host location by *G. gayi* and *Labena* sp. is similar to that typically reported for parasitoids using vibrational sounding in host searching and unlike that reported when the female uses passive vibration detection, i.e., resting the antennae on the substrate while in a stationary position in such a way that the insect listens to sounds produced by the potential host (Hanks *et al* 2001) or vibrational detection through subgenual organs in the legs (Broad & Quicke 2000, Joyce *et al* 2011). Furthermore, enlarged female subgenual organs and antennal modifications present in all species of *Labena* (Broad & Quicke 2000) and also in related parasitoids (Broad & Quicke 2000, Vilhelmsen *et al* 2001) suggest the use of vibrational sounding in the host selection process (Broad & Quicke 2000, Vilhelmsen *et al* 2001). Hence, we suggest that *G. gayi* and *Labena* sp. detect concealed individuals of *M. postica* developing inside nests by means of vibrational sounding. However, the use of semi-chemicals for habitat location (e.g., finding of a potential host–plant while flying) should not be ruled out.

Parasitized nests of *M. postica* were larger in length and diameter than unparasitized nests, suggesting that gallery dimensions represent nest parameters that influence the oviposition preferences of *G. gayi* and *Labena* sp. Given that larger nests contain more potential hosts, as demonstrated in this study, the selection of larger nests increases the probability to enhance parasitoid fitness due to increased opportunities for oviposition (van Baalen & Hemerik 2008). On the other hand, parasitized nests had thinner walls than unparasitized ones. This result is associated with the depth of hosts within the substrate and with the ability of the female to drill through a substrate using the ovipositor, two factors known to influence host location activities and oviposition preferences (Xiaoyi & Zhongqi 2008), suggesting that females are able to detect the thickness of walls around nests and decide to oviposit in those whose access will require less drilling efforts.

The relative proportions of parasitized and unparasitized nests of *M. postica* at any given period can be related to the life cycle of the host. Thus, at the onset of the breeding period, *M. postica* females dig a tunnel in the substrate. After that, females construct a food mass, place an egg on it, and build a partition using wood dust, a sequence which is repeated several times before the nest is completed. Therefore, the number of individuals developing inside cells increase along the breeding period (Flores-Prado *et al* 2008). This could explain the higher degree of parasitization of nests collected towards the end of the breeding period.

Vibrational sounding has been hypothesized as a feature of phylogenetically basal parasitoids (Gauld 1988, Gauld &

Wahl 2000, Broad & Quicke 2000). Not surprisingly, such a host detection mechanism appears to be used by *Labena* and *Grotea*, both genera belonging to Labeninae, a basal subfamily within the Ichneumonidae (Quicke *et al* 1999, Broad & Quicke 2000) that comprises species exhibiting several plesiomorphic traits (Gauld & Holloway 1986). On the other hand, *Manuelia* possesses several ancestral features (Michener 2000) and has been proposed as the most basal taxon in the phylogeny of Xylocopinae (Flores-Prado *et al* 2010), which in turn is the most basal subfamily of the Apidae (Michener 2000). Additionally, a Gondwanan origin has been hypothesized for both Labeninae and Xylocopinae (Gauld & Holloway 1986, Engel 2001) and both the parasitoid species and the host species have been proposed as primitive lineages that became geographically isolated (Gauld & Holloway 1986, Daly *et al* 1987). Hence, an ancestral host–parasitoid relationship between *Manuelia*, and *Labena* sp. and *G. gayi* may be inferred making this native system an ideal model to study the adaptive significance of coadapted traits involved in the evolution of those lineages.

Finally, some hymenopteran parasitoids discover concealed hosts by exploiting chemical instead of vibrational cues. For example, *Melittobia digitata* Dahms (Hymenoptera: Eulophidae) wasps parasitize immobile prepupae of the mud dauber wasp *Trypoxylon politum* Say (Hymenoptera: Crabronidae) which are located inside mud nests. Volatiles emitted by recently built nests, which do not appear in the mud from old nests, attract the parasitoids to their surroundings (Cusumano *et al* 2010). It has been hypothesized that chemicals associated with female mouthparts of *T. politum*, the structures used to manipulate mud and build a nest, could be acting as a kairomone, thus explaining why fresh mud is attractive but old mud is not (Cusumano *et al* 2010). Following such hypothesis, it is possible that the entrance of *M. postica* nests, which are constructed by female bees with their mouthparts, contains chemicals that may be used by the ichneumonid parasitoids to detect their host nests. It would be interesting to explore the presence of such chemicals at the entrance of *M. postica* nests and assess their involvement in parasitoid attraction.

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