

Research

Effects of Body Size on the Biological Fitness of a Koinobiotic Phorid Parasitoid and on the Parasitoid–Termite Host Relationship

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Abstract

The relationship between the solitary koinobiont endoparasitoid *Misotermes mindeni* Disney and Neoh (Diptera: Phoridae) and its termite host *Macrotermes gilvus* (Hagen) (Termitidae: Macrotermitinae) was examined. *Misotermes mindeni* were reared from parasitized *M. gilvus* major soldiers in the laboratory. Adult female parasitoids were on average larger (4.67 ± 1.29 mg) than males (3.73 ± 1.18 mg). The influence of the size of the parasitoid on its fitness was studied under laboratory conditions. No relationship was found between adult female size and the number of laid eggs, but weak positive relationship was observed between adult male size and longevity. The sex of emerging adults of *M. mindeni* was correlated positively with the size of the major soldiers of *M. gilvus*. Females emerged from the larger hosts, whereas males emerged from the smaller hosts. The host size ranges differed between the sexes. This may suggest that the parasitoids modified the size of their hosts. The body sizes of both female and male parasitoids at pupal and adult stages were significantly correlated with host size, such that larger hosts ultimately yielded larger parasitoids and smaller hosts yielded smaller ones.

Key words: *Misotermes mindeni*, *Macrotermes gilvus*, Diptera, morphological change

Body size is an important indicator of parasitoid fitness or quality (Croft and Copland 1995, Sagarra et al. 2001), including fecundity, longevity, development time, host-finding ability, and mating success (e.g., Visser 1994, Lampson et al. 1996, Hegde and Krishna 1999, Morrison et al. 1999, Kolluru and Zuk 2001, Sagarra et al. 2001, Lykouressis et al. 2009, Kant et al. 2012, Saeki and Crowley 2013, Sreekanth and Muralimohan 2013, Segoli and Rosenheim 2015). As a general rule, larger parasitoids are characterized by greater fitness than smaller ones (Charnov 1979, Van den Assem et al. 1989, Jenner and Kuhlmann 2006). Several studies have emphasized that the fitness of a given parasitoid increases profoundly with body size. For example, larger females may oviposit more eggs during their lifetime and in turn produce more progeny and they are expected to live longer and have higher host searching efficiency than smaller females, and larger males may benefit from higher mating success and longer life span (e.g., Visser 1994, Lampson et al. 1996, Hegde and Krishna 1999, Morrison et al. 1999, Kolluru and Zuk 2001, Sagarra et al. 2001, Lykouressis et al. 2009, Kant et al. 2012, Saeki and Crowley 2013, Sreekanth and Muralimohan 2013, Segoli and Rosenheim 2015).

In many host–parasitoid systems, the sex of emerging parasitoids correlates positively with host size: Females tend to emerge from

larger hosts and males from smaller ones (King 1987, Gunasena et al. 1989, Morrison et al. 1997, Morrison and Gilbert 1998, Folgarait et al. 2005). A positive relationship between host and parasitoid size has also been found in koinobiotic parasitoid species across orders (i.e., the larger the host, the larger the size of the parasitoids; Gunasena et al. 1989, Kouame and Mackauer 1991, Tillman and Cate 1993, Morrison and Gilbert 1998).

Misotermes mindeni Disney and Neoh (Diptera: Phoridae) is a solitary koinobiont endoparasitoid of the fungus-growing termite *Macrotermes gilvus* (Hagen) (Termitidae: Macrotermitinae) in Malaysia. Parasitization of *M. gilvus* by *M. mindeni* begins at the fourth larval instar (L4) stage and continues through the major pre-soldier and major soldier stages (Neoh and Lee 2010, Foo et al. 2011a). The first parasitoid larval instar completes its development in L4s and major presoldiers. The larva moves freely within the host body cavity and head capsule. Second and third instars persist in the head capsule and abdomen of major soldiers, respectively (Foo et al. 2011a). By the time the fly larva is ready to pupate, it has consumed the entire content of the soldier head capsule and has moved to the host's abdomen. Subsequently, the fly larva contracts intensively and applies sideways pressure to pierce the abdominal wall of the

major soldier. The termite body fluids ooze out, leaving a dry microhabitat for pupation. The host dies once pupation is completed (Neoh and Lee 2010). The development duration of *M. mindeni* from first larval instar until pupation is ~56 d, and it takes the pupa ~14 d to emerge as an adult (Foo et al. 2011a).

Many aspects of the biology of *M. mindeni* and the interactions between the parasitoid and its host remain largely unexplored. In this study, we addressed the following questions: 1) Does parasitoid size influence parasitoid fitness? and 2) Are the sex and size of the parasitoids at pupal and adult stages correlated with host size?

Materials and Methods

Termite Host Collection and Maintenance

Parasitized major soldiers were obtained from six previously surveyed colonies of *M. gilvus* on the Minden Campus of Universiti Sains Malaysia (5° 21' N, 100° 18' E), Penang, Malaysia (Foo et al. 2011c). Parasitized hosts were identified by their rounded head capsules with remarkably short mandibles (Neoh and Lee 2010). *Macrotermes gilvus* mounds were partially opened by digging a trench around the base of the nest. Sideways pressure was subsequently applied to remove the outer wall casing in a careful manner to avoid injury to parasitized major soldiers, which were often congregated at the peripheral zone of the mound (Neoh and Lee 2010, Foo et al. 2011c). Collected parasitized major soldiers together with major and minor workers and fungus comb were maintained in a plastic container (18.0 by 12.0 by 6.0 cm) in an incubator (Incucell, MMM Medcenter Einrichtungen GmbH, München, Germany) at 28 ± 1°C and 90% relative humidity (RH) under constant darkness. Sand with 20% moisture content was provided as a medium. Parasitized hosts were held for the emergence of adult *M. mindeni*.

Size-Related Parasitoid Fitness

In this study, fecundity and longevity were selected as measures of female and male parasitoid fitness, respectively. The relationship between adult female size and fecundity was examined with 64 female-male pairs. The female abdomen has the tergites incomplete and ill-defined and ends in with the long and narrow, telescopic, ovipositor segments, while male has well-developed and well-defined tergites and a small compact hypopygium (epanfrum and hypandrium embracing the penis complex and a protruding anal tube; Disney et al. 2009). Total body length (TBL; from head to the tip of the abdomen) of the adult females was measured upon emergence. The pairs then were kept in individual Petri dishes (5.5 cm in diameter, 1.5 cm in depth) and supplied with 10% sucrose solution ad libitum. The flies were kept in an incubator at 28 ± 1°C and 90% RH. Fecundity was measured by counting the number of eggs laid per female until the flies died.

The relationship between adult male size and longevity was investigated with newly emerged adult males ($n=57$). TBL of adult males was measured. They were confined individually in the manner described above. Observations were made daily to record the mortality of the adult flies. Adult longevity was defined as the time interval from adult eclosion until death.

Sex and Size of the Parasitoid Pupae and Adults in Relation to Host Size

Experiments were conducted to study the possible correlations between host size and sex and size of *M. mindeni* parasitoids at pupal and adult stages. Once pupae appeared in the abdomens of hosts, the following measurements were taken from the termite hosts (Fig. 1) using Analysis Image Processing software (Soft Imaging

System GmbH, Münster, Germany) mounted under a SZ61 stereomicroscope (Olympus, Tokyo, Japan) equipped with IC Imaging Standard V2.1 (The Imaging Source Europe, Bremen, Germany): 1) head width (HW); 2) head width to side base of mandibles (HWSM); 3) head length to side base of mandibles (HLSM); 4) pronotum length (PL); 5) pronotum width (PW); 6) mesonotum width (MW); and 7) metanotum width (MeW) ($n=145$). No significant differences in size were detected between freshly collected and dead parasitized major soldiers ($P > 0.05$).

Fly pupae were measured concurrently for length (PuL; from tip to the distal part) and width (PuW; measured as its widest point; $n=145$). After measurement, fly pupae were placed individually in glass vials (5 cm long, 2.5 cm in diameter) with a vented lid. Moistened sand in the base ensured humidity during pupation. Vial lids were covered with a mesh screen to prevent escape of flies upon emergence. Fly pupae were then incubated at 28 ± 1°C and 90% RH. Pupation was completed in ~2 wk. Emerged flies were sexed and measured. TBL was used as an index of adult fly size ($n=49$ for females and $n=66$ for males). Adult females and males were then weighed to the nearest 0.01 mg with a digital analytical balance (Sartorius BP 190S, Goettingen, Germany).

Statistical Analysis

We used Student's t-test to compare the weight of female and male adult flies. Comparisons of host and pupal size between adult female and male flies were conducted with the same statistical test. Spearman's rank correlation test was used to describe the relationship between host and pupal size and sex of emerging adult flies. The relationship between host size and parasitoid size at the pupal and adult stages was assessed using polynomial quadratic regression analysis, and polynomial linear regression analysis was used to determine the relationships between adult female size and fecundity and between adult male size and longevity. Most analyses were performed using SPSS version 16.0 for Windows (SPSS Inc., Chicago, IL), but SigmaPlot version 10.0 for Windows (Systat Inc., Chicago, IL) was used for regression analyses. $P < 0.05$ was considered to be significant for all analyses.

Results

Size-Related Parasitoid Fitness

Adult females began to oviposit during the first day after eclosion. No relationship was found between adult female size and the number of laid eggs. A significant positive relationship was also detected between adult male body size and longevity, but the association was relatively weak (Fig. 2).

Sex and Size of the Parasitoid Pupae and Adults in Relation to Host Size

The average (mean ± SD) fresh weight of adult females (4.67 ± 1.29 mg, range = 2.30–7.20 mg, $n=24$) was significantly greater than that of males (3.73 ± 1.18 mg, range = 1.80–7.50 mg, $n=23$; $t=2.522$; $df=45$; $P < 0.01$). The hosts from which females emerged were larger than those in which males developed (Table 1). The sex of emerging *M. mindeni* adults was significantly correlated with the size of the parasitized major soldiers of *M. gilvus* (Tables 1 and 2). Adult female parasitoids developed in larger host and males developed in smaller ones (Table 1).

Tables 3–8 show the relationship between host size and size of the parasitoid (females and males) at pupal and adult stages. Parasitoid size was significantly correlated with host size, such that larger hosts ultimately yielded larger phorid parasitoids and smaller

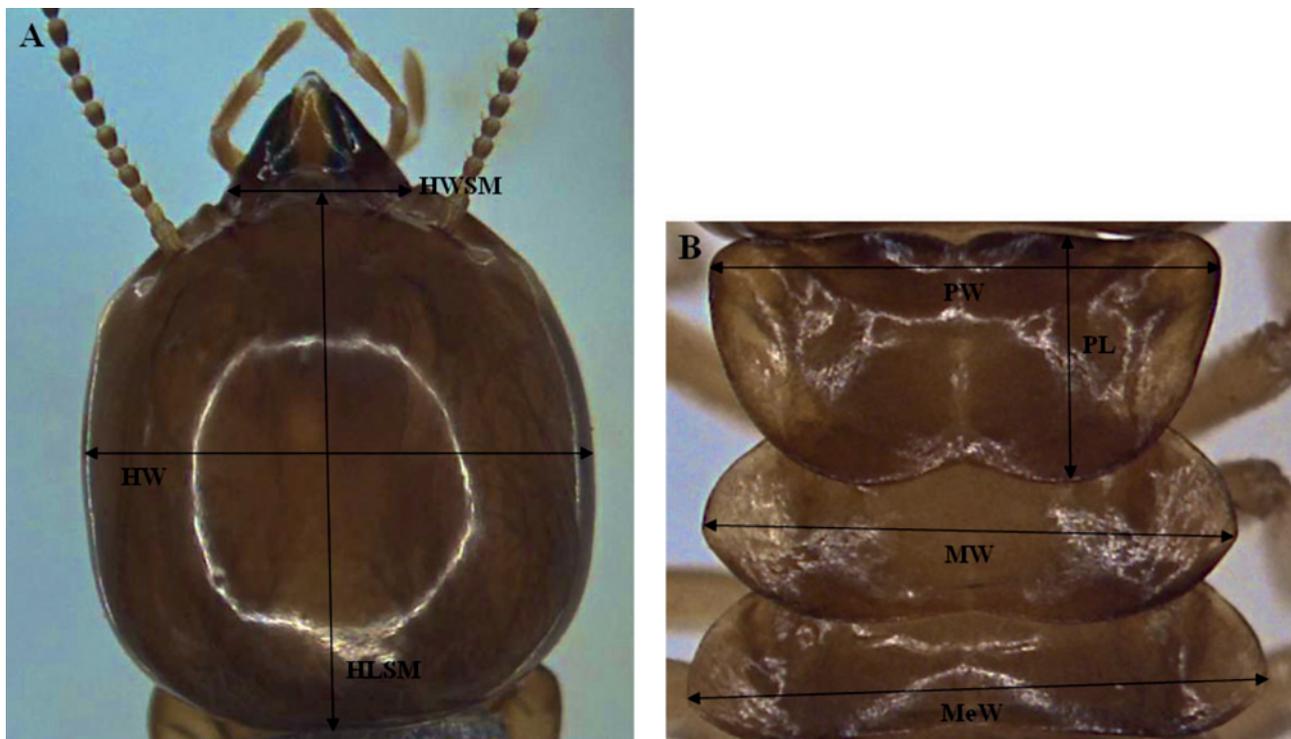


Fig. 1. Diagram of measured parts of a parasitized *M. gilvus* major soldier. (A) HW, head width; HWSM, head width to side base of mandibles; HLSM, head length to side base of mandibles. (B) PL, pronotum length; PW, pronotum width; MW, mesonotum width; MeW, metanotum width.

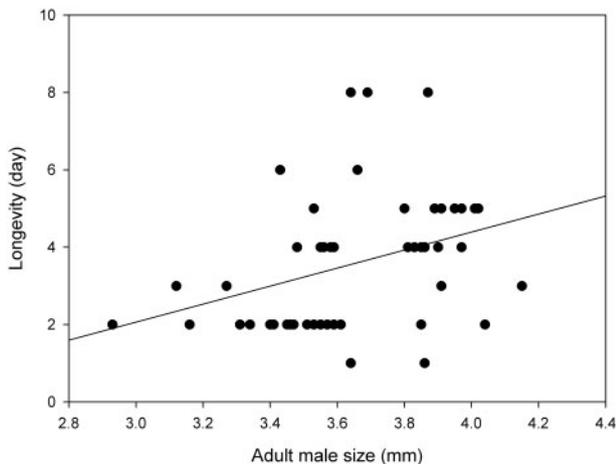


Fig. 2. Relationship between adult male size, measured by total body length (TBL), and longevity (d) [$y = 2.33x - 4.92$, where x = adult male size (mm), y = longevity (d), $r = 0.35$; $r^2 = 0.12$; $n = 47$; $P < 0.05$].

hosts yielded smaller ones. A quadratic regression model was preferred over a linear regression model because the former better explained the variance for each parasitoid sex.

Discussion

Size-Related Parasitoid Fitness

Sexual size dimorphism is a frequent phenomenon in animals (Salvo and Valladares 1995, Harvey and Strand 2003). It is also true for *Pseudacteon* phorid flies, the solitary endoparasitoid of *Solenopsis* fire ants, with females generally being larger than males (Morrison et al. 1999). Based on fresh weight, we found that females of the phorid *M.*

mindeni tend to be larger than male conspecifics. Perhaps such a difference with respect to sex may be attributed to egg production by the females, which need to accumulate greater reserves, as egg laying commenced within a day of emerging. This premise is further supported by the fact that parasitized major soldiers of *M. gilvus* contain greater lipid reserves than unparasitized ones (Foo et al. 2011b).

Several studies have shown that larger females may oviposit more eggs during their lifetime and in turn produce more progeny and they are expected to live longer and have higher host searching efficiency than smaller females, and larger males may benefit from higher mating success and longer life span (e.g., Visser 1994, Lampson et al. 1996, Hegde and Krishna 1999, Morrison et al. 1999, Kolluru and Zuk 2001, Sagarra et al. 2001, Lykouressis et al. 2009, Kant et al. 2012, Saeki and Crowley 2013, Sreekanth and Muralimohan 2013, Segoli and Rosenheim 2015). However, results of the current study do not support these observations, as we found that larger female flies were incapable of laying more eggs and longevity was weakly associated with adult male size. Similar observations of weak association between male size and longevity have been reported for the ichneumonid endoparasitoid *Campoplex dubitator* Horstmann that parasitizes the moth *Enarmonia formosana* Scopoli (Jenner and Kuhlmann 2006). Blackburn (1991) studied the significance of body size and ecological factors on parasitoid life history variations and concluded that body size is not a primary determinant of adult life span.

Sex and Size of the Parasitoid Pupae and Adults in Relation to Host Size

We found a significant positive correlation between host size and the sex of the parasitoid it was carrying. Females eclosed from larger hosts and males eclosed from smaller hosts. This suggests that the sex of *M. mindeni* may influence the size of its host. A similar

Table 1. Comparison of host and pupal size between adult female and male flies, *M. mindeni*

	Female			Male			Student's <i>t</i> -test		
	<i>n</i>	Mean ± SD (mm)	Range (mm)	<i>n</i>	Mean ± SD (mm)	Range (mm)	<i>t</i>	df	<i>P</i>
Head width (HW)	58	3.50 ± 0.11	3.32–3.77	88	3.26 ± 0.18	2.31–3.61	9.225	144	<i>P</i> < 0.01
Head length to side base of mandibles (HLSM)	56	3.60 ± 0.24	2.98–4.09	87	3.39 ± 0.26	2.62–3.85	4.780	140	<i>P</i> < 0.01
Pronotum length (PL)	54	1.23 ± 0.76	1.05–1.35	81	1.20 ± 0.74	0.92–1.34	2.246	133	<i>P</i> < 0.05
Mesonotum width (MW)	55	2.52 ± 0.22	2.06–3.19	80	2.45 ± 0.15	2.15–2.85	2.164	87	<i>P</i> < 0.05
Metanotum width (MeW)	57	2.78 ± 0.19	2.40–3.26	79	2.70 ± 0.16	2.27–3.00	2.750	134	<i>P</i> < 0.01
Pupal length (PuL)	56	4.06 ± 0.14	3.70–4.39	79	3.76 ± 0.12	3.48–4.02	13.366	133	<i>P</i> < 0.01
Pupal width (PuW)	56	2.85 ± 0.12	2.46–3.06	79	2.62 ± 0.16	2.29–3.52	9.431	133	<i>P</i> < 0.01

Table 2. Correlation between host and pupal size and sex of emerging adult flies, *M. mindeni*

Host and Pupal size	<i>N</i>	<i>r</i>	<i>P</i>
Head width (HW)	145	0.72	<i>P</i> < 0.01
Head length to side base of mandibles (HLSM)	143	0.35	<i>P</i> < 0.01
Pronotum length (PL)	135	0.21	<i>P</i> < 0.05
Mesonotum width (MW)	135	0.20	<i>P</i> < 0.05
Metanotum width (MeW)	136	0.24	<i>P</i> < 0.01
Pupal length (PuL)	135	0.77	<i>P</i> < 0.01
Pupal width (PuW)	135	0.73	<i>P</i> < 0.01

phenomenon was reported by Gunasena et al. (1989) for the *Heliothis virescens* (F.)/*Camponotus sonorensis* (Cameron) host–parasitoid system, in which the parasitoids modified the size of their hosts. However, many studies have reported a different scenario (i.e., the sex of parasitoid progeny is determined by host size), particularly among the solitary parasitic Hymenoptera (Arthur and Wylie 1959, King 1987). Host size-dependent sex determination is generally well known from solitary idiobiotic parasitoids that attack nongrowing host stages (eggs and pupae) or paralyze their hosts at oviposition (King 1987). The resources of the hosts are fixed, thus such parasitoids are able to assess the quality of the host and predict its future growth from its larval stage (Salvo and Valladares 1995, Harvey and Strand 2003). In contrast, most of the koinobiotic parasitoids attack larval stage hosts that continue to grow following parasitism and whose size changes considerably between oviposition and completion of parasitoid development (Mackauer and Sequeira 1993). Moreover, host selection by koinobionts is based on the potential of the host to support the growth and development of the parasitoid rather than depending on the host size, as the selection is influenced by the host's age and development stage which determine the host's potential to support the growth of the parasitoid (Kouame and Mackauer 1991). Until recently, only one relevant case had been reported for koinobiont phorid parasitoids: *Pseudacteon* spp., which parasitizes *Solenopsis* workers, where the laboratory studies of sex allocation revealed that more females arising from larger hosts (Morrison et al. 1999). However, the hosts are highly

polymorphic, with the largest workers being three times the length of the smallest workers (Porter and Tschinkel 1985). At present, it may be difficult to provide a conclusive evidence for this because the mechanism by which *M. mindeni* enters the termite host still remains unknown.

The positive relationship between the size of the host and the size of the parasitoid found in this study was previously reported for a few other koinobiotic species of parasitoids such as *Camponotus sonorensis*, *Ephedrus californicus*, *Bracon mellitor*, and *Pseudacteon* flies (Gunasena et al. 1989, Kouame and Mackauer 1991, Tillman and Cate 1993, Morrison and Gilbert 1998) although some authors reported otherwise (Guillade and Folgarait 2011). Host size was positively correlated with the size of *M. mindeni* parasitoids at pupal and adult stages, suggesting a possible influence of host size on parasitoid size. Increased or decreased nutrient availability in the host may be responsible for this positive relationship (Gunasena et al. 1989, Tillman and Cate 1993). Another possibility is that the parasitoid induces morphological changes in the host such that larger female/male parasitoids may cause the hosts to grow larger and vice-versa. This premise is further supported by Foo et al. (2011b), who reported that parasitized major soldiers of *M. gilvus* were significantly larger (41.1%) than unparasitized major soldiers. Alternatively, manipulation of the host's physiology by the parasitoid may also be responsible for this host–parasitoid size relationship (Vinson and Iwantsch 1980). Foo et al. (2011b) recently documented several physiological changes in *M. gilvus* major soldiers induced by *M. mindeni*. For example, parasitized hosts were found to contain greater body lipid reserves than unparasitized ones, perhaps due to the requirements of the parasitoids to complete their life cycle (particularly female flies that engage in egg production). The relationship between host size and size of *M. mindeni* at pupal and adult stages was nonlinear. Salvo and Valladares (1995) stated that even though parasitoid adult size often increases with the host size, this relationship might not necessarily be a linear function of host size because the linearity in the relation is based on the pattern of parasitoid larval development.

In conclusion, body size of the parasitoid *M. mindeni* was shown to have no influence to female fecundity and the correlation between male longevity and parasitoid size was relatively weak. Sex of the

Table 3. Relationship between host size and adult female size (as measured by total body length [TBL])

Host measured parts	<i>n</i>	<i>r</i>	<i>r</i> ²	Quadratic regression	<i>P</i>
Head width (HW)	49	0.55	0.30	$y = 2.24x^2 - 13.73x + 24.95$	<i>P</i> < 0.01
Head width to side base of mandibles (HWSM)	48	0.44	0.19	$y = -8.30x^2 + 22.18x - 10.36$	<i>P</i> < 0.05
Head length to side base of mandibles (HLSM)	48	0.47	0.22	$y = 0.85x^2 - 5.4x + 13.04$	<i>P</i> < 0.01
Pronotum width (PW)	48	0.43	0.19	$y = -3.81x^2 + 20.37x - 22.80$	<i>P</i> < 0.05

x = host size (mm); *y* = adult female size (mm).

Table 4. Relationship between host size and female pupal size (as measured by pupal length [PuL])

Host measured parts	<i>n</i>	<i>r</i>	<i>r</i> ²	Quadratic regression	<i>P</i>
Head width (HW)	56	0.44	0.19	$y = 0.60x^2 - 3.61x + 9.36$	$P < 0.01$
Head width to side base of mandibles (HWSM)	48	0.44	0.19	$y = -8.30x^2 + 22.18x - 10.36$	$P < 0.05$
Head length to side base of mandibles (HLSM)	55	0.41	0.16	$y = 0.33x^2 - 2.17x + 7.57$	$P < 0.05$
Pronotum width (PW)	53	0.35	0.12	$y = -1.09x^2 + 5.87x - 3.81$	$P < 0.05$
Mesonotum width (MW)	53	0.37	0.14	$y = -0.10x^2 + 0.75x + 2.84$	$P < 0.05$
Metanotum width (MeW)	54	0.41	0.17	$y = -0.54x^2 + 3.26x - 0.81$	$P < 0.05$

x = host size (mm); *y* = female pupal size (mm).

Table 5. Relationship between host size and female pupal size (as measured by pupal width [PuW])

Host measured parts	<i>n</i>	<i>r</i>	<i>r</i> ²	Quadratic regression	<i>P</i>
Head width (HW)	56	0.34	0.12	$y = -0.82x^2 + 6.13x - 8.57$	$P < 0.05$
Head length to side base of mandibles (HLSM)	55	0.51	0.26	$y = 0.40x^2 - 2.66x + 7.26$	$P < 0.01$
Pronotum width (PW)	53	0.41	0.17	$y = -0.32x^2 + 1.98x - 0.09$	$P < 0.05$

x = host size (mm); *y* = female pupal size (mm).

Table 6. Relationship between host size and adult male size (as measured by total body length [TBL])

Host measured parts	<i>n</i>	<i>r</i>	<i>r</i> ²	Quadratic regression	<i>P</i>
Head width (HW)	66	0.52	0.27	$y = 0.42x^2 - 1.61x + 4.36$	$P < 0.01$
Head width to side base of mandibles (HWSM)	63	0.39	0.15	$y = -1.06x^2 + 3.67x + 0.74$	$P < 0.05$
Head length to side base of mandibles (HLSM)	65	0.52	0.27	$y = 0.12x^2 - 0.19x + 2.92$	$P < 0.01$
Pronotum width (PW)	61	0.48	0.23	$y = 0.29x^2 - 0.41x + 2.82$	$P < 0.01$
Mesonotum width (MW)	61	0.34	0.12	$y = -0.93x^2 + 5.19x - 3.45$	$P < 0.05$

x = host size (mm); *y* = adult male size (mm).

Table 7. Relationship between host size and male pupal size (as measured by pupal length [PuL])

Host measured parts	<i>n</i>	<i>r</i>	<i>r</i> ²	Quadratic regression	<i>P</i>
Head width (HW)	79	0.63	0.40	$y = 0.42x^2 - 2.08x + 6.04$	$P < 0.01$
Head length to side base of mandibles (HLSM)	78	0.30	0.09	$y = 0.23x^2 - 1.35x + 5.73$	$P < 0.05$
Pronotum length (PL)	70	0.38	0.14	$y = 1.52x^2 - 2.95x + 5.10$	$P < 0.01$
Pronotum width (PW)	72	0.32	0.11	$y = 0.34x^2 - 1.40x + 5.12$	$P < 0.05$

x = host size (mm); *y* = male pupal size (mm).

Table 8. Relationship between host size and male pupal size (as measured by pupal width [PuW])

Host measured parts	<i>n</i>	<i>r</i>	<i>r</i> ²	Quadratic regression	<i>P</i>
Head width (HW)	79	0.45	0.20	$y = 0.19x^2 - 0.65x + 2.77$	$P < 0.01$
Head length to side base of mandibles (HLSM)	78	0.33	0.11	$y = 0.51x^2 - 3.21x + 7.62$	$P < 0.05$
Pronotum width (PW)	72	0.32	0.10	$y = -0.34x^2 + 2.03x - 0.33$	$P < 0.05$

x = host size (mm); *y* = male pupal size (mm).

parasitoid may influence the host size, and the latter is closely related to the size of *M. mindeni* parasitoids at pupal and adult stages. This finding suggests that the parasitoid may induce morphological changes in the host, as larger female or male parasitoids may cause the hosts to grow larger, and vice-versa. However, the present finding is inconclusive, as the mechanism of parasitism on how *M. mindeni* enters the termite host remains unknown due to cryptic lifestyle of *M. gilvus*, low parasitism rate in most of the termite colonies, short life span of adults of *M. mindeni*, and

laboratory culture of *M. mindeni* larvae are nearly impossible, etc. There are several possibilities of how the larval parasitoid comes into contact with its host. First, the egg may be ingested by the target host and subsequently hatch in the host's intestine. The larva then may penetrate through the intestinal wall and enter into the host's hemolymph. Another possibility is that the hatched larva penetrates through the host's abdominal wall and enters into the host's hemolymph. More studies on the above should be carried out in future to confirm these possibilities.

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