



RESEARCH ARTICLE - WASPS

Consequences of Parasitized Prey Provision on the Fitness and Development Parameters of a Solitary Wasp, *Rhynchium brunneum brunneum* (Vespidae: Eumeninae)

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Abstract

The solitary wasp, *Rhynchium brunneum brunneum* (Fabricius), constructs nests in hollow cavities of bamboo, provisions her brood cells with caterpillars, and partitions the cells using mud. The wasp larva, upon hatching, feeds on the provisioned lepidopteran larvae and completes its development inside the cell. The fitness and development of immature stages of the wasp on the prey parasitized by *Dolichogenidea* sp. (Braconidae: Microgastrinae) was studied. The number of cells with parasitized prey was significantly higher during September (6.60 ± 0.11 parasitized prey/cell), October (9.20 ± 2.77 parasitized prey/cell), November (9.10 ± 2.59 parasitized prey/cell), and December (9.00 ± 2.01 parasitized prey/cell). The percentage of healthy prey per cell ranged between 53.33% to 100%, and parasitized prey per cell ranged from 0 to 25% in the sampled nests. The mortality of late instar wasp larvae (50 to 80%) was higher in the cells provisioned with the parasitized prey. The number of prey larvae provisioned per cell was significantly higher in the healthy cells (9.80 ± 0.84 prey/cell) compared to the unhealthy cells (3.60 ± 0.55 prey/cell). The prey biomass in the healthy cells (0.592 g) was significantly higher than in the unhealthy cells (0.161 g). The emergence percentage of the adults was significantly higher in the healthy nests (100%) than in unhealthy nests (38.67%). The study confirms the inability of the adult wasp to discriminate between healthy and parasitized prey. The adult wasp compensated for the fitness of her immature stages by collecting a mixture of healthy prey with parasitized prey to favor the growth and development of her broods in the nest.

INTRODUCTION

The solitary wasp *Rhynchium brunneum brunneum* constructs nests in hollow cavities of bamboo provisions her brood cells with caterpillars and partitions the cells using mud (Iwata, 1964; Dang & Nguyen, 2019; Udayakumar et al., 2022). The wasp larva, upon hatching, feeds on the provisioned lepidopteran larvae and completes its development inside the cell (Spradbery, 1973; Iwata, 1976; Cowan, 1991). The adult wasp gnaws through the mud partition and emerges from the nest. Eumenine wasps are efficient predators of lepidopteran larvae (Klein et al., 2004). *Ancistrocerus gazella* (Panzer) (Hymenoptera: Vespoidea: Eumeninae) was reported as an efficient predator of leafrollers *Planotortrix octo* (Dugdale),

P. excessana (Walker), *Ctenopseustis obliquana* (Walker), *Ctenopseustis herana* (Felder & Rogenhofer), and *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) infesting fruit crops in New Zealand (Harris, 1994). Investigating the factors that affect the fitness and development of the wasp's immature stages is vital for its reproduction and survival in agroecosystems. Feeding and developing eumenine larvae on parasitized prey might result in the development of smaller-sized adult wasps that negatively affect the hunting ability and survival of the progeny wasps (Cowan, 1981). Body biomass and flight abilities were reported to be vital parameters of prey-hunting solitary wasps, and feeding on parasitized insect prey will impact these fitness parameters and affect the survival of the wasps (Freeman, 1981).



The effect of lepidopteran larval prey parasitized by polyembryonic parasitoid *Copidosoma primulum* (Mercet) on the growth and development of the caterpillar hunting wasp, *Delta dimidiatipenne* (Saussure) was reported by Segoli et al. (2020). Predatory wasps, though, were reported to lack the ability to discriminate between healthy and parasitized prey (Matthews & Matthews, 2009); the cost of poor selection on the fitness of her progeny needs to be studied further. The nesting activity of *R. brunneum brunneum* was noticed in the trap nests. We observed lesser emergence of adult wasps from the occupied trap nests built by *R. brunneum brunneum*. When the occupied trap nests were opened and investigated, it was observed that braconids parasitized lepidopteran prey in some of the cells and dead immature stages of *R. brunneum brunneum*. There were no published systematic studies conducted on the effect of parasitized larval prey on the growth and development of *R. brunneum brunneum* across the globe. Keeping the ecological importance of solitary eumenine wasps as bio-control agents of economically important lepidopteran insect pests, the present study was conducted to investigate the pattern of provisioning lepidopteran prey parasitized by *Dolichogenidea* sp. (Braconidae: Microgasterinae) in the nests built by *R. brunneum brunneum* and the growth and development of immature stages of *R. brunneum brunneum* that developed on the parasitized prey.

MATERIALS AND METHODS

Study site

The present study was carried out from June 2021 to May 2023 on the experimental farm of ICAR-National Bureau of Agricultural Insect Resources (NBAIR) Bengaluru, Yelahanka Campus (13.096792N, 77.565976E), Karnataka, India.

Installation of trap nests

Paper straws of 19.5 cm in length and 12 mm in diameter were collected from local retail stores. The straws were tied into bundles using plastic thread and placed in the 'Bee Home' at the study site. Five bundles, each with ten straws, were considered five replicates for the studies.

The pattern of provision of parasitized prey in the nests of *R. brunneum brunneum*

The trap nests were observed at intervals of two days for the nest construction activity by *R. brunneum brunneum*. The trap nest entrance capped with a mud layer indicated a nest built by *R. brunneum brunneum*. The occupied trap nests were collected and taken to the laboratory. In the laboratory, the trap nests were given a delicate and gentle cut longitudinally using a sharp blade to split open and observe the inner contents of the nest. After the trap nests were opened, the cells were inspected for the prey larvae. The nest with all the cells provisioned with healthy prey was considered a healthy nest (Fig 1). The nest with one or a few cells provisioned with parasitized prey was considered an unhealthy nest (Fig 2). The number of healthy and unhealthy nests sampled from June 2021 to May 2023 was recorded. The number of larvae per cell in healthy and unhealthy nests was recorded. The number of nests provisioned with parasitized caterpillars during the nesting period was observed and recorded. The number of healthy and parasitized prey per cell was recorded. Thirty-one cells were examined. The percentage of healthy, parasitized, and mixed (healthy + parasitized) prey per cell was calculated. The mortality rate of the developing wasp larvae in the cells provisioned with healthy and parasitized prey was calculated by taking the ratio of the number of wasp larvae that died per nest with the total number of wasp larvae. The mortality trend in the early and late instar developing wasp was recorded.

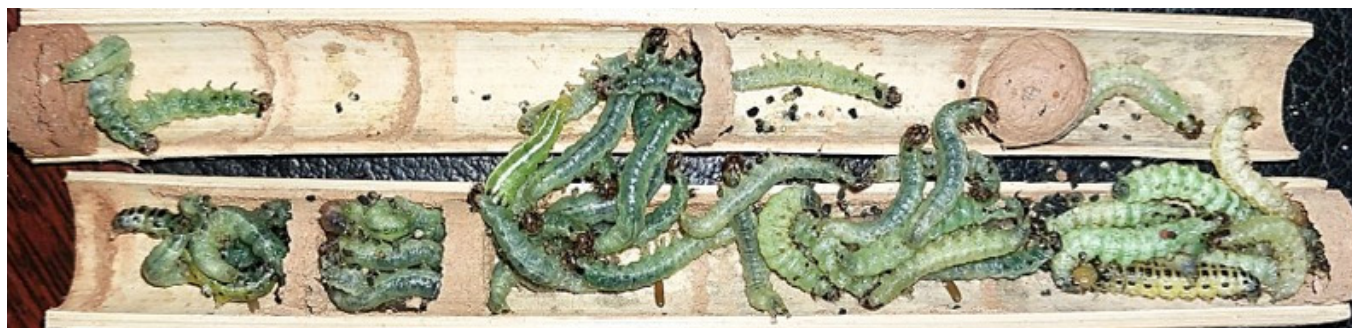


Fig 1. Healthy nests built by *R. brunneum brunneum* with cells provisioned with healthy prey.



Fig 2. Unhealthy nests built by *R. brunneum brunneum* with cells provisioned with parasitized prey.

Development of wasp larvae on the parasitized prey larvae

The effect of parasitized prey larvae on the growth and development of *R. brunneum brunneum* was studied. The survival percentage of the wasp larvae was recorded by taking the ratio of the total number of wasp larvae per nest to the number of live mature larvae after maturity. Mortality of the wasp larvae inside the cells, if any, was observed and recorded. The body mass (g) of the wasp larvae and pupae was recorded by sampling the live weight of the final instar larvae and pupae with an electronic weighing balance. The ratio of adult wasps that emerged with the total number of cells was calculated for both “healthy” and “unhealthy” cells to study the percent adult emergence.

Data analysis

The mean \pm SD of the number of nests provisioned with parasitized larvae, the number of healthy and unhealthy cells, and the placement pattern of healthy and parasitized larvae/cells were calculated. Analysis of variance (GLM in SAS 9.3; SAS Institute, Cary, NC) was used to compare the number of prey larvae provisioned per cell, wasp larva mass (g), duration of wasp larva development (days), survival rate of larvae (%), pupal mass (g) and adult emergence rate (%) between the healthy and unhealthy cells. Where significant difference was detected, treatment means were separated using Tukey’s HSD Test (0.05%).

RESULTS

The pattern of provision of parasitized prey larvae in the nests of *R. brunneum brunneum*

The wasp constructed 4 to 5 cells in both healthy and unhealthy nests. The mean number of nests provisioned with parasitized larval prey differed significantly across the different nesting periods from June 2021 to May 2023 (F value = 28.52; $P < 0.0001$) (Fig 3). Provisioning of a significantly higher number of parasitized larval prey was observed during September (6.60 \pm 0.11 parasitized prey/cell), October (9.20 \pm 2.77 parasitized prey/cell), November (9.10 \pm 2.59 parasitized prey/cell) and December (9.00 \pm 2.01 parasitized prey/cell). None of the cells built by the wasp were provisioned with parasitized larvae during March, April, and May. The mean number of parasitized larvae provisioned per cell during June and July was 0.60 \pm 0.08 parasitized prey/cell and 0.41 \pm 0.01 parasitized prey/cell, respectively. The mean number of healthy nests sampled was highest during January (5.02 nests), February (5.10 nests), March (8.52 nests), April (11.03 nests) and May (9.50 nests) (Fig 4). On the contrary, the mean number of unhealthy nests sampled was the highest during August (4.51 nests), September (2.15 nests), October (5.50 nests), November (4.56 nests) and December (6.05 nests).

Based on the visual observations, the authors also noticed a single species of prey larvae inside the cells in the unhealthy cells provisioned with parasitized prey. In contrast,

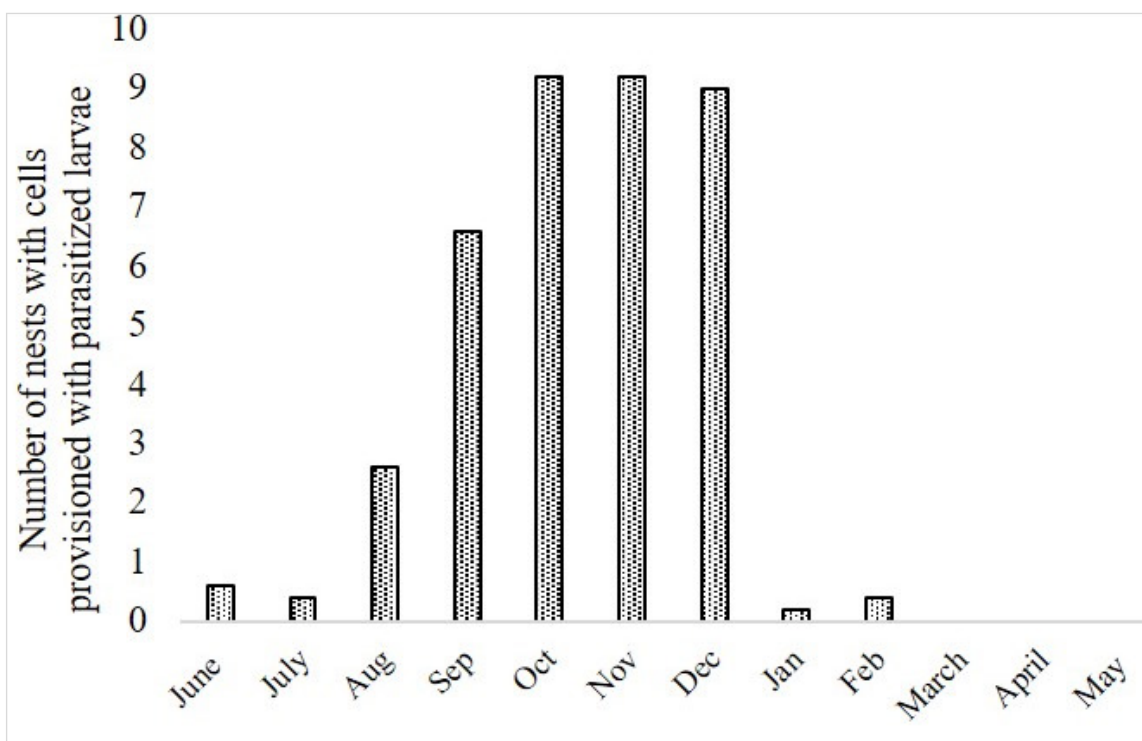


Fig 3. Trap nests provisioned with parasitized larval prey across the nesting period.

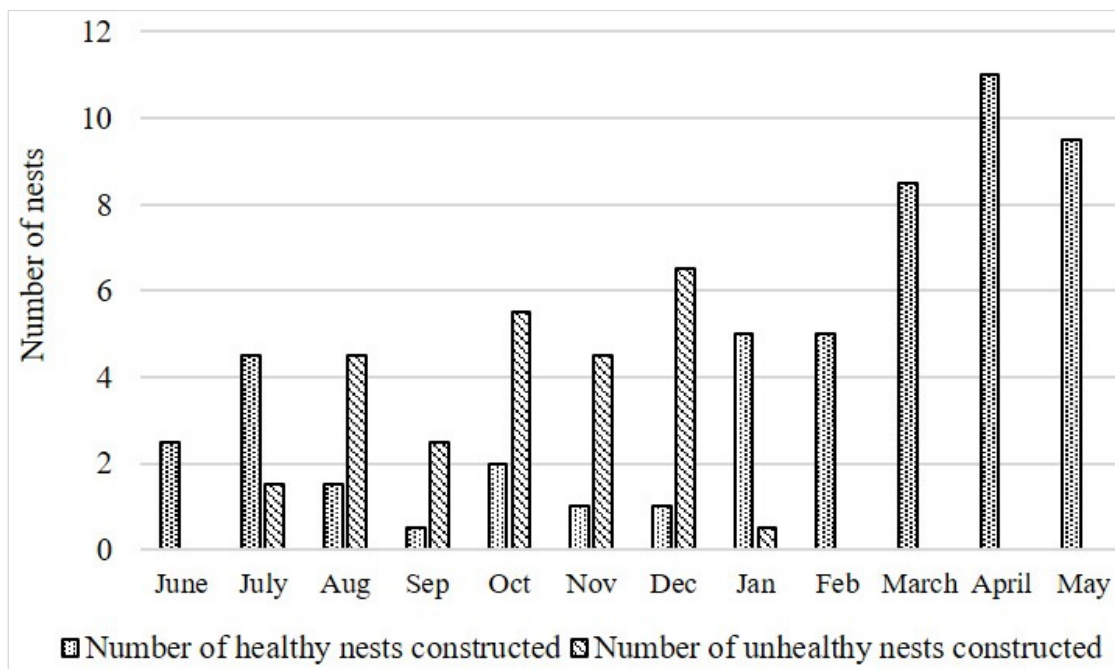


Fig 4. Number of healthy and unhealthy nests sampled during the study period.

a mixture of 2-3 different species of larvae was observed in the healthy cells. The healthy and parasitized prey provision pattern per cell was observed and recorded (Fig 5). Of the 31 sampled cells inside the nest built by *R. brunneum brunneum*, the percentage of healthy larvae per cell ranged between 36.79% (N6 – Nest 6) to 100% (N8 – Nest 8), percentage of the parasitized larvae per cell ranged between 25% (N5 – Nest 5) to 46.15% (N4 – Nest 4) and the percentage of mixed (healthy + parasitized) prey larvae ranged between 0.24% (N4 – Nest 4) to 10% (N7 – Nest 7). The percent mortality of early instar wasp larvae in the cells provided with healthy and parasitized prey ranged between 25% and 60%. On the contrary, higher mortality of late instar larvae of the wasp was recorded, ranging between 50 to 80% (Fig 6).

Development of wasp larvae on the parasitized prey larvae

The development and mortality of wasp larvae feeding inside the parasitized prey-provisioned cells are given in Table 1. The number of prey larvae provisioned per cell differed significantly between healthy and unhealthy nests (F value = 11.30; $P < 0.001$). A significantly higher number of larval prey were provisioned in the healthy nests (9.80 ± 0.84 prey/cell) than in unhealthy nests (3.60 ± 0.55 prey/cell). There was a significant difference in the survival rate of the wasp larvae in the cells with healthy and parasitized prey (F value = 66.44; $P < 0.001$). The highest survival rate of the wasp larvae was recorded in the cells with healthy prey (95.01%) compared to those with parasitized prey (34.17%). Average wasp larval

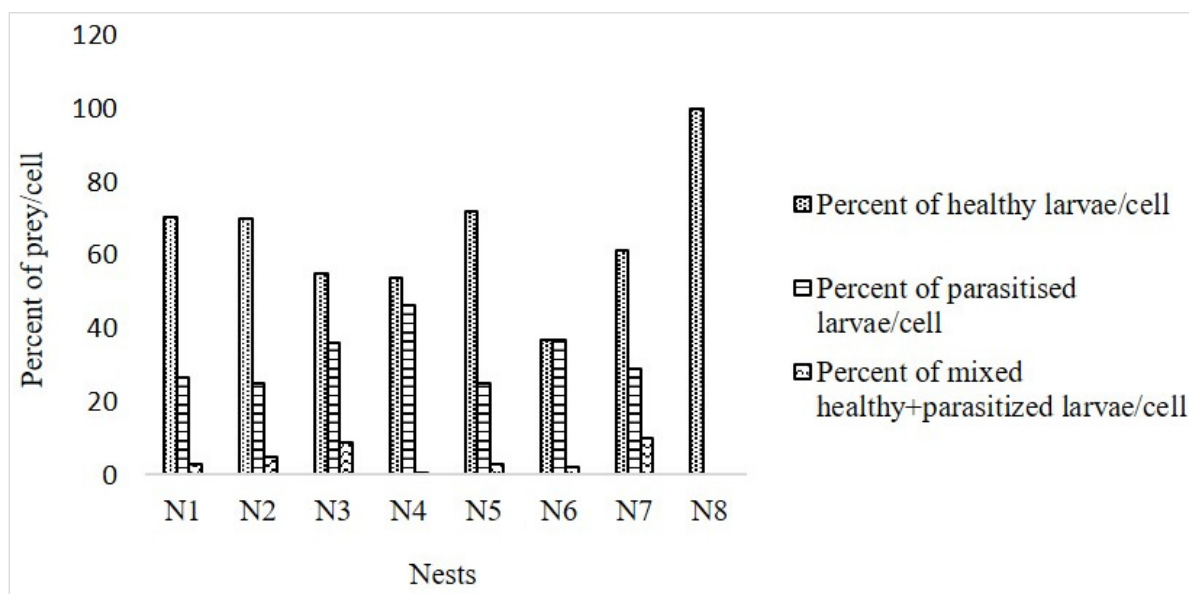


Fig 5. Pattern of healthy, parasitized and mixed larval prey per cell built by *R. brunneum brunneum*.

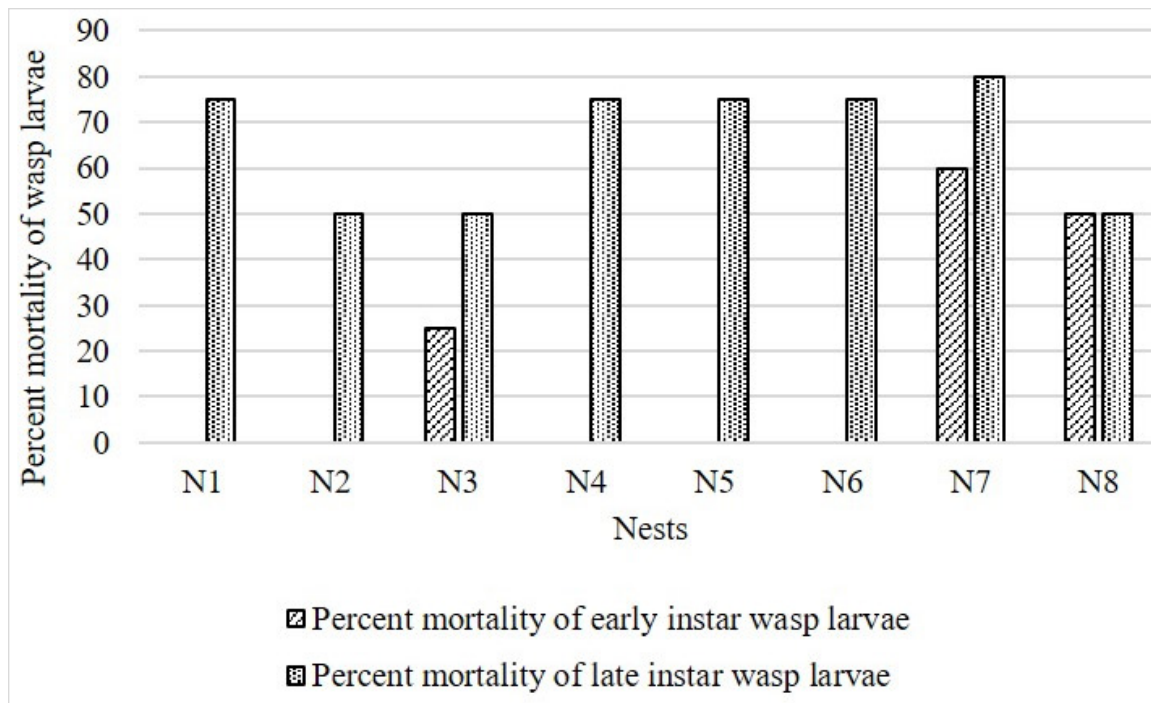


Fig 6. Mortality in the early and late instar larvae of *R. brunneum brunneum*.

mass differed significantly in the nests provisioned with healthy and parasitized prey (F value = 12.57; $P < 0.001$). The average mass (g) of the final instar wasp larvae was significantly higher in the cells provisioned with healthy prey (0.592 g) compared to the larvae observed in the cells with parasitized prey (0.161 g). There was a significant difference in the duration of development of larvae in the cells provisioned with healthy and parasitized prey (F value = 53.33; $P < 0.001$). The larval development was significantly faster in the cells provisioned with healthy prey (5.60 ± 0.55 days) than in the cells provisioned with parasitized prey (9.61 ± 1.51 days). The pupal weight of the wasp differed significantly between the cells provisioned with healthy and parasitized prey (F value = 18.19; $P < 0.001$). The pupal mass was significantly higher in the healthy nest (0.368g) compared to the unhealthy nest (0.096 g). Adult emergence rates differed significantly between the cells provisioned with healthy and parasitized prey (F value = 9.04; $P < 0.001$). The mean adult emergence per cell was 100% in the cells provisioned with healthy prey compared to a significantly lesser emergence rate in the cells provisioned with parasitized prey (38.67%).

DISCUSSION

The adult wasp was observed to provision her broods with healthy prey larvae from January to May. Nests with parasitized prey larvae were recorded from August to December. The wasp provisioned a mixture of healthy and parasitized larvae in a few cells. This showed maternal care for her brood, ensuring fair diet availability for a brief period upon hatching rather than complete starvation. The mortality of the later instar wasp larvae was higher compared to the early instar wasp larvae in most of the sampled nests, indicating that the wasp larvae, after consumption of healthy larvae provisioned in each cell during its early stages of development, might have starved for a healthy prey larva during its later instars and died inside the cells.

The authors, while observing the unhealthy nest with parasitized prey in the cells, noticed later instar larvae of braconids (Fig 7) or pupated braconids (Fig 8) around the larval prey, which was unfit for consumption by the larval stage of the wasp. The reason could be that the adult wasp would have hunted pre-parasitized prey larvae with braconid parasitoids

Table 1. Development of wasp in the healthy and unhealthy cells.

Nests	Number of prey larvae provisioned/cell	Wasp larva mass (g)	Duration of wasp larva (days)	Wasp larva survival rate (%)	Wasp pupa mass (g)	Adult wasp emergence rate (%)
Healthy cells	9.80 ± 0.84	0.592a	$5.60 \pm 0.55b$	95.01a	0.368a	100
Unhealthy cells	3.60 ± 0.55	0.161b	$9.61 \pm 1.51a$	34.17b	0.096b	38.67
F value	11.30	12.57	53.33	66.44	18.19	9.04
P value	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$

Means followed by same letter do not differ significantly from each other by Tukey's HSD at 0.05% level of significance.

at its final stage of development, which would have formed a cocoon inside the cells. The highest mortality rate of the wasp larvae might be due to the non-availability of quality prey for feeding, which leads to ‘hunger death’. The non-consumption of the prey larvae parasitized by *Copidosoma primulum* and non-emergence of an adult potter wasp, *Delta dimidiatipenne*, due to low-quality prey was reported by Johnson et al. (2023).

The larger parasitized prey larva would have been a ‘preferred hunting prey’ for the foraging wasps, with a relatively lower number of foraging flights required to provision each cell. The authors hypothesize that the wasp would have preferred fewer foraging bouts by collecting larger parasitized prey at the cost of the development of her brood. The foraging of parasitized prey could be a hunting tactic of the adult wasp as the parasitized prey were immobile and lethargic due to pre-parasitization, thereby offering minimum resistance during the hunting by the wasp. The immobile pre-parasitized larvae will be easy to hunt and handle by the foraging wasps compared to the healthy smart prey that will handle escape mechanisms to avoid predation risk under field conditions.



Fig 7. Prey larva showing mature gregarious grub of *Dolichogenidea* sp. on its body surface.



Fig 8. Prey larva showing braconid pupae of *Dolichogenidea* sp. on its body surface.

The immobile and fragile nature of the larvae parasitized by braconid owing to the internal development of the parasitoid was reported by Lekha Priyanka et al. (2022). Leduc et al. (2022) reported less responsiveness of the parasitized prey during the simulated potter wasp predator attack, making it more susceptible to predation.

Moreover, the adult wasp did not exhibit significant nest-guarding behavior during the nest construction process. We observed the activity of sarcophagid flies (unidentified) near the nests when the adult wasp was out for her prey foraging trip. Hence, the wasp might not have exercised any selective foraging tactics for the healthy prey under field conditions. She would have resorted to quick prey foraging trips back to her nest to avoid nest parasites. Sarcophagid flies (Miltogramminae) are nest parasites that affect the emergence of adult eumenine wasps from the cells, as Spofford et al. (1989) reported.

The developing wasp larvae recorded significantly lower mass in the unhealthy cells. The lack of sufficient healthy prey for the developing wasp larvae might be a strong reason for the lower mass buildup and survival rate of the wasp larvae in the unhealthy cells. The larvae with lesser mass often were observed to develop into a “miniature-adult” wasp in some of the cells. Coincidentally, pupal mass was significantly lowest in the unhealthy nests with parasitized prey. Small-sized wasps compromise their flight abilities for prey hunting and foraging and are less reproductively fit than average adults, negatively impacting their nest-building ability (Beukeboom, 2018). The results were in line with the findings by Leduc et al. (2022), who reported the reduced development of potter wasp larvae when provisioned with parasitized prey. The results of the present study were in line with the observations made by Segoli et al. (2020), who recorded significantly lower masses of larvae and pupae of the wasp in the cells provided with parasitized prey. The duration of development of wasp larvae was relatively faster in the healthy nests compared to the unhealthy nests with parasitized prey. One of the reasons for the prolonged development of larvae feeding on the parasitized prey might be the low-quality nutrition provided by the parasitized prey during its development. A more extended development period of *Coccinella septempunctata* (Linnaeus) when reared on parasitized aphid was reported by Chatha and Naz (2020).

The wasp provisioned more prey larvae/cells in the healthy cells and fewer prey larvae/cells in the unhealthy cells. The parasitized prey with the immature stages of gregarious braconid larvae developing inside the caterpillar appeared larger than the average healthy larval prey. We observed that the provisioning of 3-4 larger parasitized prey occupied the entire cell space, and the adult wasp might hardly have any space for further provision of larvae in the cells. On the contrary, with healthy prey being slender, regular, and uniform in size, the wasp provisioned more prey larvae per cell in the ample space available for 8-9 prey in the healthy nests.

Larvae of army cutworm, *Euxoa auxiliaries* (Grote) parasitized by *Copidosoma bakeri* (Howard) were reported to be higher in body mass than healthy larvae (Byers et al., 1989).

CONCLUSION

The results of this study confirmed the inability of the adult solitary wasp, *R. brunneum brunneum*, to discriminate between the healthy and parasitized prey larvae during her foraging bouts. However, the wasp inadvertently compensated her bad choice of prey with her maternal instinct by substituting the cells with a mixture of healthy and parasitized prey. The development of wasp larvae is absolutely a chance factor of either developing into a fit adult or hunger death during the later larval stages.

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