



## Predatory potential of two species of *Monomorium* on the developing stages of silkworm *Antheraea mylitta* (Drury) (Lepidoptera: Saturniidae)

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**ABSTRACT:** Among the predators that attack tasar silkworm, *Antheraea mylitta*, *Monomorium destructor* and *M. minimum* are serious on early larval instars as well as pupae of *A. mylitta*. Host-predator interactions were studied, including all the predatory events of the predation by a single as well as groups of ants on *A. mylitta*. Predatory risk of these ants in the field is discussed.

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**KEYWORDS:** *Antheraea mylitta*, *Monomorium*, predatory behavior, tasar silkworm

### INTRODUCTION

The tropical silkworm, *Antheraea mylitta* (Drury) (Lepidoptera: Saturniidae) is primarily reared on *Terminalia tomentosa* synonym *T. elliptica* Willd. and *T. Arjuna* (Roxb.) W. & A and it produces a unique variety of wild 'Tasar' silk (Jolly *et al.*, 1968, 1979). It has three crops in a year, and though it is wild by nature, it is being exposed to several threats during its life span (Jolly *et al.*, 1968, Singh and Thangavelu, 1991). The abundance of the predators in the tasar rearing sites directly affects the wild tasar silk production (Singh and Thangavelu, 1991). However, among the predators, the ants are also affecting the Indian sericulture industry (Negi *et al.*, 1993; Gathalkar and Barsagade, 2016 a), as well as several other commercially important insects (Gosswald, 1990; Hölldobler and Wilson, 1990; Petal, 1978; Risch and Carroll, 1982). Similarly, the ant species, viz. *Pheidolegeton diversus* (Jerdon), *Monomorium minutum* (Mayr) and *Myrmecaria brunnea* (Saunders) are also

documented as a predator of tasar and muga silkworms both (Negi *et al.*, 1993; Gathalkar and Barsagade, 2016 a). Whereas, *Monomorium minimum* (Buckley), and *Pheidole* sp. are known to attack the temperate tasar silkworm, *Antheraea proylei* (Jolly) (Negi *et al.*, 1993). Similarly, the ant *Tapinoma melanocephalum* (Fabricius) is attacking the pupae and adults of the muga silkworm (Singh 1991, Negi *et al.*, 1993). While, *Polyrhachis bicolor* (Smith) recognized to drag the spinning larvae, in a group (Bidyapati *et al.*, 1994). The ant species such as *Tetraoponera rufonigra* (Jerdon), *Camponotus compressus* (Fabricius) and *Oecophylla smaragdina* (Fabricius) are very frequent foragers in the tasar rearing fields (Singh, 1991; Gathalkar and Barsagade, 2016 a,b; Negi *et al.*, 1993) by which the tasar silk production is being reduced.

The myrmicine genus *Monomorium* is one of the most influential groups of ants regarding its abundant diversity, intra-morphological and biological

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variability (Aslam *et al.*, 2006). Of these, *Monomorium pharaonis* (Linnaeus), *Monomorium destructor* (Jerdon), and *Monomorium floricola* (Jerdon) are well-known domestic pests (Williams, 1994). As predators of various pest species, they also are used in pest management system. In addition, some ants are essential for the pollination, predation, scavenging, soil improvement, nutrient cycling as well as plant dispersal (Gotwald, 1986; Folgrait, 1998; Lach *et al.*, 2010). There are 358 species, and 27 subspecies have been listed in the genus *Monomorium* (Bolton, 2016). Mostly the several species of ant are acting like a pest in the various fields and urban habitats (Vega and Rust, 2003). In urban populations, ants cause frequent pest problems where they destroy the aesthetic and economic value of many products of human consumption (Hölldobler and Wilson, 1990; Lee, 2002). These ant species also act as vectors of various plant diseases, whereas, the attack of some ant species is quite painful to domestic animals as well as human beings (Vinson, 1986; Goddard and de Shazo, 2004). However, the ant species are also used as an ecological indicator, to assess the ecological status, concerning species diversity and the impact of invasive species (Bharti *et al.*, 2016), rather most of them are standard generalized predators of many tropical crops (Aslam *et al.*, 1994). Subsequently, the weaver ant *O. smaragdina* is the highly aggressive predator in tasar sericulture, as well as it is also used as a biological control agent in many commercial crops (Way and Khoo, 1991; Paulson and Akre, 1992). Similarly, these predatory ants are also helpful in controlling a variety of insect pests of various crops in temperate and tropical areas, such as cocoa, pears, cotton and rice (Way and Khoo, 1991; Paulson and Akre, 1992). Generally, the soil-dwelling ant species are known to feed on many like earthworm, acarid, isopod, myriapod, collembolan, termite, beetle, bark lice and lepidopteran species (Cerda and Dejean, 2011). Subsequently, many studies have been conducted on the foraging behavior of various ant species (Sudd, 1968; Gotwald, 1986). The ant species such as *O. smaragdina*, *Monomorium* sp. and *Pheidole* sp. are the well-known predators of the *A. mylitta*

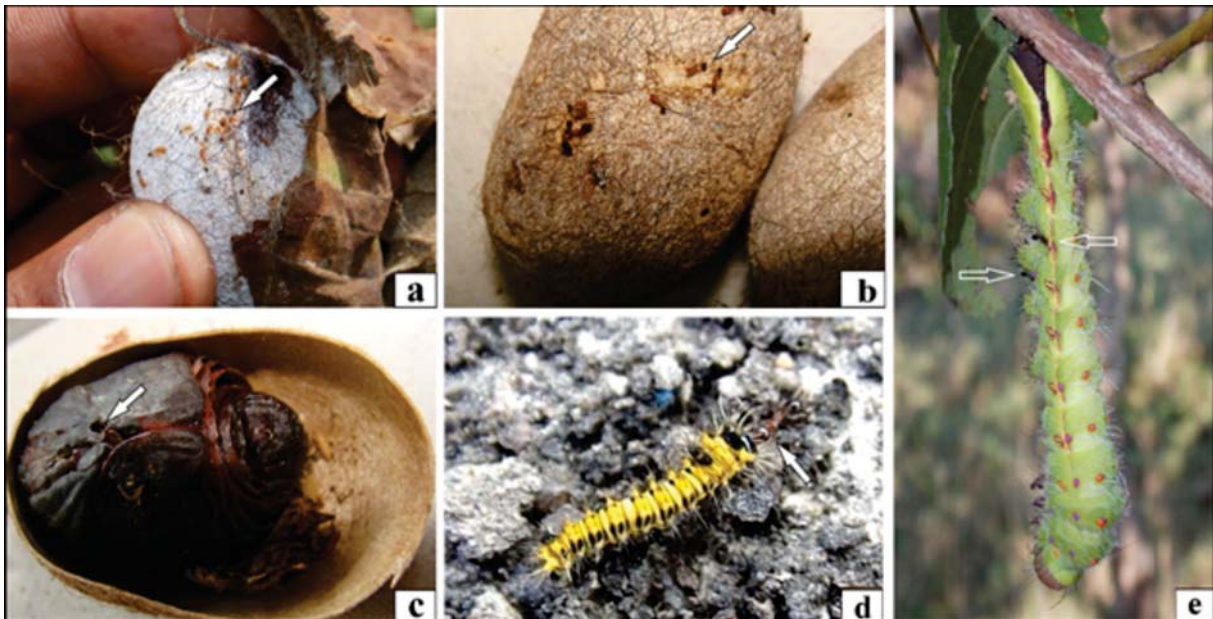
(Jolly *et al.*, 1979; Singh and Thangavelu, 1991; Singh, 1991). However, the predation biology of these ants is poorly known in the field of tasar-culture. Therefore, the present study was carried out to explore more about the predatory potential of these tiny ants especially, *Monomorium destructor* and *M. minimum* and their invasive impact on tasar-culture.

## MATERIALS AND METHODS

The tasar silkworm, *A. mylitta*, is cultivated in the tropical forests of India, and primarily reared on *Terminalia tomentosa* (Yen), *T. arjuna* (Arjun) and several other secondary food plants. *Antheraea mylitta* is the principal non-mulberry silk producing insect in the tropical forest of Vidarbha in Maharashtra. The life cycle of *A. mylitta* undergoes into the egg, five larval stages, pupa, and adult (Gathalkar and Barsagade 2016a). There are three crops, *viz.*, crop I, crop II and crop III in the months of June–August, August–October, and October–January respectively. During the study, various eco-zones of Bhandara and its adjacent districts were investigated during 2010-2013, to know the occurrences and the predation risk of pest species. In addition, all the predatory behaviour of ants including host-predator interaction and host damage were observed visually and video-graphed. Further more, the identification of ant species was made in Department of Zoology, RTM Nagpur University, Nagpur with the help of an online catalog (Bolton, 2014) and morphological characteristics.

## RESULTS

The predator belonging to family Formicidae, such as *Monomorium* (*M. minimum* and *M. destructor*) are abundant in tasar rearing fields and affecting the total silk production by attacking the defenseless stages of *A. mylitta*. These reddish-brown small sized ants are active throughout the year on the tasar host plants with their nest under the tree at ground and tree crest. The ants (workers) attack the first to third instar larvae, as well as the pupa of *A. mylitta*, through the cocoon shell by making small holes and feed complete pupa/seed (Figs 1 a-d), and causes the tasar mortality.



**Figure 1** Predation of *Antheraea mylitta* by tiny ants showing, a-b: attack of *Monomorium destructor* on the cocoon, c: damaged pupa, d: attack of *M. minimum* transporting the first instar larva e: feeding activity of *M. minimum* on the fifth instar larva of *A. mylitta*.

#### Damage level:

These tiny ants revealed the aggressive predation on the early larval instar as well as the pupae (through the cocoon shell) of the tasar silkworm, *A. mylitta*. The average mortality of all the three crops/year suggested that the early instar stages are more vulnerable to predation while the fourth and fifth stages showed very rare predation by these predators. The pupae of the silkworm also totally destroyed by the predation and pupa of silkworm became dead. The tasar mortality by these predators concerning its crop-wise mortality it is estimated up to 2-4% of crop damage, due to which production of silk is being affected.

#### Behaviour Study:

##### Feeding habits and prey distraction(Field invasion)

In tasar rearing areas, the as the ants *Monomorium minimum* and *M. destructor* have their terrestrial nests as well as the conspicuous trail on plants, including *Terminalia tomentosa* and *T. arjuna* where they feed the tasar larva. The worker ants

of these species attack many larvae of *A. mylitta*, including pupae, and kill a broad range of host stages (Figs 1 a-d). Similarly, the weaver ant *O. smaragdina* is a dangerous larval predator of *A. mylitta* was also reported during the present study. These ants have aggressive predatory habit, they attack the early instars and the pupae of silkworm. Whereas, the attack on late instar disturbed from their normal development or the entire spinning process. The highly organized, aggressive predatory behavior, combined with extensive foraging throughout the area occupied by a colony, explains the success of tiny ant species in killing or driving away many tasar silkworms. Due to the attack, early larval instar, as well as the pupae of the silkworm, get damaged totally, which affects the raw silk production. Being a predator of concealed pupae of tasar silkworm and the pores of the cocoon shell made by *Monomorium destructor* (workers), the quality of cocoons also affected (Fig. 1a-c). Some of the ants also carry their prey to their colony. Similarly, we also recorded the dare of this tiny ant *i.e.* by *M. minimum* which was carrying the first instar larva of silkworm (Fig.1d) (Sup. Info. 1: <https://youtu.be/jSycX5tAuMg>). During the



predation, the host larva trying to escape many times, but the grips of ant mandibles make the tasar larva effortless. Surprisingly, the single ant can drag the whole first instar larva of the silkworm, where the larvae trying to escape many times but the predator does not allow its single move. Sometimes, they also feed the late instar larva of *A. mylitta*, either the larva may be previously damaged by another predator, dead or diseased, where they can get an easy source of food (Fig. 1e). Due to the predation of this tiny ant, the larvae of tasar silkworm become sluggish. Further more, the death of the larva occurs. However, the pupa remains into the dead shell of the cocoon with complete destruction or dead pupa. These observations are somewhat serious and the care should be taken while the rearing of the tasar silkworm, to explore the benefit of nature blessed tasar silkworm *A. mylitta*, which provides a unique yarn for economic excellence, through the tasar-culture.

## DISCUSSION

The parasite–predator complex of the silkworm *A. mylitta* results in loss of wild tasar silk production (Gathalkar and Barsagade, 2016 a). Among the predators, the ants are also the risk factor in the tasar rearing fields. However, in the present study, it has been observed that the *Monomorium* species viz., *M. destructor* and *M. minimum* are also affecting the larval as well as pupal stages of the tasar silkworm. These ant species attack the silkworm larvae while they are feeding on the host plants, whereas, the pupae, adults and eggs are primarily affected at grainage. However, it is well-documented that the most arboreal and some terrestrial taxa forage extensively for carbohydrate-rich plant secretions and insect exudates (Hölldobler and Wilson, 1990; Davidson, 1997). Subsequently, the predatory habit of the ants has a major influence in many habitats (Wilson, 1971; Carroll and Janzen, 1973). Similarly, *O. smaragdina* is a well-known predator of *A. mylitta*. Nevertheless, it is being used as a biological control agent in various agricultural crops (Way and Khoo, 1991; Paulson and Akre, 1992; Way *et al.*, 2002). Based on ant-prey inter relationships and their foraging habit, the predacious ants can be classified as specialists or generalists

(Wilson, 1959). Most of the species are scavengers where they prey on small organisms, including the insect eggs. The specialist ant does not seem to be significant in biological control, though some must have an impact, on certain pest (Way and Khoo, 1991). The generalist ant predators include those that are recognized as important in biological control (Petal, 1978; Risch and Carroll, 1982). Most of the invasive ants are usually habitat generalists, can invade and establish themselves in undisturbed habitats (Passera, 1994). Indigenous generalist predators have been controlling pests on crops since the dawn of agriculture, and the Chinese have used ant nests into citrus orchards to monitor the pest population (Symondson *et al.*, 2002). Ant as a predator of many pests of the commercially important crops, they are also useful in pest management. It is also well documented as the ants prey on eggs as well as larvae of numerous pest species in many different countries and habitats (Way *et al.*, 1989; Weseloh, 1989; Way and Khoo, 1991).

The small red ant, *Formica rufa* (Linnaeus) also known to kill many different defoliating pests in European forests (Pascovici, 1979; Gosswald, 1990). Thus, these ants are acting as biological-control agents, some ants are important in pollination, soil improvement, and nutrient cycling (Gotwald, 1986). In contrast, some feed on/or disturb the plants and may act as vectors of some plant diseases, while their attack also causing the skin irritation of human being, domestic animals, and other beneficial organisms (Vinson, 1986; Goddard and de Shazo, 2004). In contrast, the predacious ants affect the behavior of prey directly and depress the size of potential pest populations (Rico-Gray and Oliveira, 2007). Whereas, most are the scavenger ant species prey on small organisms, including insect eggs (Way and Khoo, 1991, 1992). As a predator ants are important in biological control, and the ranges of prey species captured by these ant species (Petal, 1978; Risch and Carroll, 1982). Many insects possess generalized defense mechanisms such as flight, jumping away, or dropping off the plant when threatened, but these may not be effective against ants that forage at different levels of the ecosystem (Heads and

Lawton, 1985). Size and other physical attributes aid in prey defense (Way and Khoo, 1992). However, in terms of commercially important crop, like a silkworm rearing, the occurrence of ant species is problematic to larval as well as the pupal stage of silkworms in the tasar rearing field and grainage. The ants around and in the households, they feed any food available (Smith, 1965). *Monomorium destructor* is a small ant, and it also exhibits polymorphism and varies in size from 1.8 to 3.5 mm (Harris *et al.*, 2005). These are the common household pests, and the foragers are slow to find food compared with other tramp ants (Lee, 2002; Lee *et al.*, 2002). *M. destructor* was recorded primarily foraging in the crown of coconut trees, but it was also seen at the base of trees in Sri Lanka (Way *et al.*, 1989). They were a minor component of the ant fauna, with *M. floricola* (Jerdon), *O. smaragdina*, *Crematogaster* sp. and *Paratrechina longicornis* (Latreille) the most common ants (Way *et al.*, 1989). The attack by *O. smaragdina* (workers) is severe in tasar sericulture, where they completely tear the early larval stages of *A. mylitta*. Also, they transport their prey to their colony as observed earlier (Gathalkar and Barsagade, 2016 a,b). *Monomorium destructor* forms large polygyne colonies (Smith, 1965), where they form their nest predominantly in trees in hollow twigs and branches as well as in the soil in tropical regions (Smith, 1965). Different species adopt different foraging patterns or strategies (Ayre, 1962) with a proportion of foragers feeding on liquid food and demonstrating high trophallaxis rates (Stradling, 1978). Previous work reported that foraging workers of *Monomorium* sp. are passive-movers unlike the erratic foragers from the *Tapinorna* or *Paratrechina* genera (Edwards, 1986). Similarly, *Pheidole* sp. are the major predators of *Alabama argillacea* egg (Gravena and Pazetto, 1987). Certain cultural practices benefited with the predation some ant species, e.g., *Monomorium*, *Solenopsis*, as predators and/or scavengers of eggs and other life stages of pests (Way and Khoo, 1992), and these small ants can flourish even where other ants dominate like *O. smaragdina* (Way *et al.*, 1989).

The tasar larval destruction by the ant predators is severe, as well as the small sized pores on the cocoon caused by *M. destructor*, with broken silk thread, which is the ultimate root of the valueless cocoon. Similarly, the damaged tasar pupae, could not develop further, and next generation where the seed cocoons get permanently vanished. Therefore, the tasar mortality by these predators with respect to its crop-wise mortality it is estimated up to 2-4% of crop damage studied earlier (Gathalkar and Barsagade, 2016 a), and the production of silk is being affected. A behavioral study on *Monomorium* shows its predatory potential with the power of grasping, whereas, the larva of *A. mylitta* became defenseless. Therefore, an abundance of these ants in tasar growing areas, hamper the tasar crop production and need to have very careful about the risk. Also, the techniques related to its eradication from the tasar rearing sites need to explore further, and an electrophysiological study may be helpful in this regard to control the damage.

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## REFERENCES

- Aslam M., Shaheen F.A. and Ayyaz A. (2006) Management of *Callosobruchus chinensis* Linnaeus in Stored Chickpea through Interspecific and Intraspecific Predation by Ants. World Journal of Agricultural Sciences 2 (1): 85-89.
- Ayre G.L. (1962) Problems in using the Lincoln Index for estimating the size of ant colonies (Hymenoptera: Formicidae). Journal of New York Entomological Society 60: 159-167.
- Bharti H., Bharti M. and Pfeiffer M. (2016) Ants as bioindicators of ecosystem health in Shivalik Mountains of Himalayas: assessment of species diversity and invasive species. Asian Myrmecology 8: 1-15.
- Bidyapati L., Noamani M.K.R. and Das P.K. (1994) Pest complex of Oak tasar. Indian Silk pp. 44-48.

- Bolton B. (2014) An Online Catalog of the Ants of the World <http://antcat.org/catalog/429718>.
- Carroll C.R. and Janzen D.H. (1973) Ecology of foraging by ants. *Annual Review of Ecological System* 4: 231-57.
- Cerda X. and Dejean A. (2011) Predation by ants on arthropods and other animals. In: Polidori C. (Ed.): *Predation in the Hymenoptera: an evolutionary perspective*. TransWorld Research Network, Kerala, pp. 39-78.
- Davidson D.W. (1997) The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biological Journal of Linen Society* 61: 153–181.
- Edwards J.P. (1986) The biology, economic importance, and control of the pharaoh's ant, *Monornoriurn pharaonis* (L.). In: SB Vinson (ed.) *Economic impact and control of social insects*. Praeger Publishers, New York. pp. 257-271.
- Folgarait P.J. (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation* 7: 1221-1244.
- Gathalkar G.B. and Barsagade D.D. (2016 b) Predation biology of weaver ant *Oecophylla smaragdina* (Hymenoptera: Formicidae) in the field of tasar sericulture. *Journal of Entomology and Zoology Studies* 4(2): 07-10.
- Gathalkar G.B. and Barsagade D.D. (2016 a) Parasites–predators: their occurrence and invasive impact on the tropical tasar silkworm *Antheraea mylitta* (Drury) in the zone of central India. *Current Science* 111 (10) 1649-1657.
- Goddard J. and de Shazo R. (2004) Fire Ant Attacks on Humans and Animals. In: *Encyclopedia of Pest Management*, CRC Press doi:10.1081/E-EPM-120024662
- Gosswald K. (1990) Die Waldameise. Band 2. Die Waldameise im Okosystem Wald, ihr Nutzen und ihre Hege. Wiesbaden: Aula-Verlag. 510 pp.
- Gotwald W.H. (1986) The beneficial economic role of ants. In *Economic Impact and Control of Social Insects*, ed. Vinson SB, pp. 290-313. New York: Praeger.
- Gravena S. and Pазetto J.A. (1987) Predation and parasitism of cotton leafworm eggs, *Alabama argillacea* (Lep.: Noctuidae). *Entomophaga* 32 : 241-48.
- Harris R., Abbott K., Barton K., Berry J., Don W., Gunawardana D., Lester P., Rees J., Stanley M., Sutherland A. and Toft R. (2005) Invasive ant pest risk assessment project for Biosecurity New Zealand. Series of unpublished Landcare Research contract reports to Biosecurity, New Zealand. BAH/35/2004-1.
- Heads P.A. and Lawton J.H. (1985) Bracken, ants and extrafloral nectaries. III. How insect herbivores avoid ant predation. *Ecological Entomology* 10:29-42.
- Hölldobler B. and Wilson E.O. (1990) *The Ants*. MA: Belknap Press of Harvard University Press, Cambridge, MA. 732 pp.
- Jolly M.S., Chaturvedi S.M. and Prasad S.A. (1968) Survey of Tasar crops in India. *Indian Journal of Sericulture* 1 : 50-58.
- Jolly M.S., Sen S.K., Sonwalkar T.N. and Prasad G.K. (1979) Non-mulberry silks. *Food and Agriculture Organization of United Nations, Ser Bull* 29, 1-178.
- Lach L., Parr C.L. and Abbott K.L. (2010) *Ant Ecology*, 1edn, pp 402. Oxford University Press, Oxford.
- Lee C.Y. (2002) Tropical household ants: pest status, species diversity, foraging behaviour, and baiting studies. In: Jones, SC, Zhai, J, Robinson WH, (eds) *Proceedings of the 4<sup>th</sup> International conference on urban pests*. Virginia, Pocahontas Press. pp. 3-18.
- Lee C.Y., Lim C.Y. and Darah I. (2002) Survey on structure-infesting ants (Hymenoptera: Formicidae) in food preparative outlets. *Tropical Biomedicine* 19: 21-26.
- Negi B.K., Siddiqui A.A. and Sengupta A.K. (1993) Insect pests of Muga Silkworms and Their Management. *Indian silk*, 32 : 37-38.
- Pascovici V.D. (1979) *Especies du groupe Formica rufa L. de Roumanie et leur utilisation dans la lutte contre les ravageurs forestieres*. *Proceedings of the meeting of the working groups on Formica rufa and vertebrate predators of insects*. Bull. West Palearctic Reg. Sect. Int. Org. Biol. Control 2: 111-34. Varenna, Italy: West Palearctic Regional Section of the IOBC).
- Passera L. (1994) Characteristics of tramp species. In: *Exotic ants* (Williams D, ed), Westview Press, Boulder, 22-43.
- Paulson G.S. and Akre R.D. 1992. Evaluating the effectiveness of ants as biological control agents of pear psylla (Homoptera, Psyllidae). *Journal of Economic Entomology* 85: 70-73.
- Petal J. (1978) The role of ants in ecosystems. In: MV Brian (ed) *Production ecology of ants and termites*. IBP 13:293–325. Cambridge University Press, Cambridge
- Rico-Gray V. and Oliveira P.S. (2007) *The Ecology and Evolution of Ant-Plant Interactions*. University of Chicago Press, Chicago.

- Risch S.J. and Carroll C.R. (1982). Effect of a keystone predaceous ant, *Solenopsis geminata*, on arthropods in a tropical agroecosystem. *Ecology* 63:1979–1983.
- Singh R.N. and Thangavelu K. (1991) Parasites and Predators of Tasar silkworm *Antheraea mylitta* has many enemies. *Indian Silk* 30(7) 33-36.
- Singh K.C. (1991) Controlling the insect enemies of oak tasar silkworms. *Indian Silk*, 30 (7):19-23.
- Smith MR, 1965. Household-infesting ants of the eastern United States: their recognition, biology, and economic importance. Washington, U.S. Department of Agriculture Technical Bulletin 1326. 105pp.
- Stradling D.J. (1978) Food and feeding habits of ants. In: M.V. Brian (ed.) *Production ecology of ants and termites*. Cambridge University Press, Cambridge 81- 106 pp.
- Sudd J.H. (1968) *An introduction to the behaviour of ants*. Department of Zoology, The University Hull, Edward Arnold Publish. LTD. London.
- Symondson W.O.C., Sunderland K.D. and Greenstone M.H. (2002) Can generalist predators be effective Biocontrol agents? *Annual Reviews of Entomology* 47:561–94.
- Vega S.Y. and Rust M.K. (2003) Determining the foraging range and origin of resurgence after treatment of Argentine ants (Hymenoptera: Formicidae) in urban areas. *Journal of Economic Entomology* 96:844-849.
- Vinson S.B. (ed), 1986. *Economic Impact and Control of Social Insects*. New York: Praeger. 421 pp.
- Way M.J. and Khoo K.C. (1991) Colony dispersion and nesting habits of the ants, *Dolichoderus thoracicus* and *Oecophylla smaragdina* (Hymenoptera: Formicidae), in relation to their success as biological control agents on cocoa. *Bulletin of Entomological Research* 81: 341-350.
- Way M.J. and Khoo K.C. (1992) Role of Ants in Pest Management. *Annual Reviews of Entomology* 37:479-503.
- Way M.J., Cammell M.E., Bolton B. and Kanagaratnam P. (1989) Ants (Hymenoptera: Formicidae) as egg predators of coconut pests, especially in relation to biological control of the coconut caterpillar, *Opisina arenosella* Walker (Lepidoptera: Xyloryctidae), in Sri Lanka. *Bulletin of Entomological Research* 79:21 9-33.
- Way M.J., Javier G. and Heong K.L. (2002) The role of ants, especially the fire ant, *Solenopsis geminata* (Hymenoptera: Formicidae), in the biological control of tropical upland rice pests. *Bulletin of Entomological Research* 92: 431-437.
- Weseloh R.M. (1989) Simulation of predation by ants based on direct observations on gypsy moth larvae. *Canadian Entomologist* 121: 1069-1076.
- Williams D.F. (1994) Control of the introduced pest *Solenopsis invicta* in the United States, pp. 282-291 in D. F. Williams [ed.] *Exotic ants*. Westview, Boulder, Colorado.
- Wilson E.O. (1959) Some ecological characteristics of ants in New Guinea rain forests. *Ecology* 40:437-47.
- Wilson E.O. (1971) *The Insect Societies*. Cambridge, MA: Belknap. 548 pp.

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