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Consumptive and Non-consumptive Effects of a Generalist and a Specialist Arthropod Predator on Ant-tended Aphids

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Abstract: The present study sheds light on the consumptive effects (CEs) and the non-consumptive effects (NCEs) of a generalist, *Oxyopes javanus* Thorell, and a specialist arthropod predator, *Coccinella transversalis* Fabricius, on an aphid, *Aphis gossypii* Glover, a pest of an extrafloral nectar-bearing, *Clerodendrum infortunatum* L. plant. Our results revealed that the percentage of aphids consumed (i.e. CE) by the two species of arthropod predators was significantly higher in the absence of the two species of plant-visiting ants, *Camponotus compressus* (Fabricius) and *Crematogaster subnuda* Mayr, than in the presence of either of the two ant species. Further, the ladybird beetle, *Coccinella transversalis* consumed a significantly higher percentage of aphids in the presence of the ant *Crematogaster subnuda* than in the presence of *Camponotus compressus*, indicating the differential effects of the two ant species on the CEs of the aphidophagous ladybird beetle. The NCEs of the predators on the aphids was insignificantly higher in the absence of both of the ant species. The inclusion of ants along with the two species of arthropod predators in the experimental arena significantly reduced the anti-predatory escape response exhibited by the aphids. This suggests that the facultative ant-aphid mutualistic association influences the CEs as well as the NCEs of the arboreal predators on the aphid pests. These results have significant implications in the use of arthropod predators as biocontrol agents in the management of honeydew producing hemipteran pests, under field conditions.

Keywords: Facultative mutualistic association, Spider, *Oxyopes javanus*, Aphidophagous ladybird beetle, *Coccinella transversalis*, Extrafloral nectary-bearing plants, *Crematogaster subnuda*, *Aphis gossypii*, *Clerodendrum infortunatum*

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Introduction

Ants belonging to several genera, such as *Camponotus*, *Crematogaster*, *Oecophylla* etc. include ground-dwelling and/or arboreal ant species, the foragers of which, visit plants that provide sugary plant-based resources such as extrafloral nectar and honeydew (Rico-Gray and Oliveira, 2007; Kumari and Rastogi, 2018). Hence,

the sap-sucking aphids and the arboreal foraging ants often co-occur on the same plants. The plant-derived carbohydrate resources are the most commonly used currencies in ant-plant and ant-hemipteran mutualistic associations (Rudolf and Palmer, 2013). The plant-visiting ants may obtain rich carbohydrate resources directly from the

extrafloral nectaries (EFNs) of plants (Ekka and Rastogi, 2019) or indirectly by interacting with the aphids, the latter being phloem feeders can easily provide the reward in the form of the excreted honeydew. Hence, both the highly active ant foragers, searching for the easily accessed caloric reward and the vulnerable and sedentary aphids have adapted by evolving a facultative mutualistic association, in which the aphid-tending ants collect honeydew from aphids and in return they provide protection from predators and parasitoids (Delabie, 2001; Stadler and Dixon, 2005; Nelsen *et al.*, 2018). Ants with species-specific differences in their defensive and aggressive capabilities may be involved in the facultative mutualistic association with aphids (Ness *et al.*, 2006; Mooney and Mandal, 2010; Senft *et al.*, 2017).

Many species of plants infested with insect herbivores (for instance, the sap-sucking aphids), are visited by both generalist predators, such as the spiders (Gavish-Regev *et al.*, 2009) as well as by specialist predators, like the aphidophagous ladybird beetles, both of which exhibit a substantial consumptive effect (CE) mediated via direct predation of the aphid prey (Dixon, 2000; Thomine *et al.*, 2020). Spiders are one of the commonly occurring arthropod predators in the terrestrial ecosystems and are reported to play an important role in keeping insect herbivore populations in check on a wide variety of plants, including those of economic importance (Lefebvre *et al.*, 2017; Michalko *et al.*, 2019; Mishra and Rastogi, 2020). The intra-guild competitions may sometimes lower the efficiency of these biocontrol agents (Liang *et al.*, 2021). When aphid-infested plants bearing EFNs attract aggressive ants, the interspecific interactions may involve not only the arthropod predators but also the aphid-tending ants. Interestingly, many EFN-bearing plants attract diverse predatory arthropods, including spiders, wasps and ladybird beetles apart from the aggressive ant guards (Agarwal and Rastogi, 2010; Del-Claro *et al.*, 2016). Further, several recent studies have emphasized the importance of non-consumptive effects (NCEs) of arthropod

predators on insect herbivores, in insect pest management (Thaler and Griffen, 2008; Hermann and Landis, 2017). The NCEs, sometimes also referred to as risk or fear effects, are reported to affect the physiology and behaviour of the potential prey due to stress induced by the presence of the potential predator (Mitchell and Harborne, 2020). Most species of aphids respond to 'fear factors' such as predator presence or to predator-associated cues (Khudr *et al.*, 2017) by showing anti-predatory defensive behaviour by walking away or by dropping down from the host plant (Harrison and Pressier, 2016)

Clerodendrum infortunatum Linn. (Family: Lamiaceae), is a wild, perennial shrub of medicinal importance, which grows in several parts of India (Bhattacharjee *et al.*, 2011). Our preliminary field observations revealed that *C. infortunatum* plants host a species rich arthropod assemblage, comprising herbivores, predators and ants. The cotton aphid, *Aphis gossypii* Glover, an important pests of many crop plants (Gissella *et al.*, 2006; Singh *et al.*, 2014) was found to be most abundant among the insect herbivores, while the arthropod predators included the lynx spider, *Oxyopes javanus* Thorell (Araneae: Oxyopidae) and the ladybird beetle, *Coccinella transversalis* Fabricius (Coleoptera: Coccinellidae). Two species of ants (Formicidae), *Camponotus compressus* (Fabricius) and *Crematogaster subnuda* Mayr were found to be the most common and abundant EFN-visiting species. Since the composition of arboreal assemblage on this EFN-bearing plant provides a situation where the co-occurring members of various guilds are likely to interact with each other, it provides a system to find whether the consumptive and non-consumptive effects of the arthropod predator on the aphid pest are affected by the presence of the aphid-tending worker ant visitors on *C. infortunatum* plants. The findings have important implications in the management of the aphid pest by the biological control approach.

In the present study, the following three interrelated questions were addressed: (i) Are the

consumptive (i.e. predaceous) effects of the lynx spider and the ladybird beetle on the aphid, *A. gossypii*, affected by the presence of each of the two aphid-tending ant species? (ii) Do the aphids show differential response to the presence of each of the two species of predators, under ant-excluded and -included conditions? (iii) Does the presence of the aphid-tending ants influence the non-consumptive effects of the arthropod predators on the potential aphid prey?

Materials and Methods

In order to examine the influence of ant-aphid mutualism on the CE and NCEs of the arthropod predators on the aphids, experiments were designed in a Petri dish arena. The experiments were conducted during February, 2020 under laboratory conditions within an hour of collection of the various species of arthropod visitors of *C. infortunatum* plants. The arthropods belonging to the various trophic levels, including the two species of arthropod predators (*Oxyopes javanus* and *Coccinella transversalis*), minor caste worker ants (i.e. the foraging caste) of two species (*Camponotus compressus* and *Crematogaster subnuda*) and the aphid (*Aphis gossypii*) were collected from the plants (during the flowering season), growing under natural field conditions in the Botanical Garden of Banaras Hindu University, Varanasi, U.P., India. The four categories of experiments included: (1) control (in which both species of predators were excluded) and three sets of treatment experiments (involving only one or both the predator species) as follows: (2) predator I (including only spider, *O. javanus*) (3) predator II (including only ladybird beetle, *C. transversalis*), and (4) both predators (including both *O. javanus* and *C. transversalis*). Each set (of these four categories of experiments) was conducted under three different conditions (n=15, in each case) by: (i) excluding both the ant species, (ii) including only *C. compressus* ants, and (iii) including only *C. subnuda* ants. Aphids (n=50, in each case) naturally present on a single twig of *C. infortunatum*, were gently introduced (without

disturbing the aphids in any way) in each Petri dish. Thus, in the control group, no predators were present; a single individual spider, *O. javanus* was introduced in each Petri dish of 'Predator I' group. In the same way, a single beetle, *C. transversalis* was introduced in each Petri dish of 'Predator II' group. One individual each of the spider and the beetle were introduced in each Petri dish experiment of 'both predators' category. All arthropod predators were starved for 24 h prior to the experiment.

The escape behaviour of the aphids under each condition was assessed by recording the number of aphids (at 3 hourly intervals for 9 h, after introduction of the arthropods in each Petri dish) that dropped off the twig onto the base of the Petri dish. The mortality of the aphids, due to the CE and NCEs of the two species of predators, under different ant-exclusion and -inclusion conditions, in different experimental categories, was recorded after 24 h in each case.

The mortality of aphids through CE and NCE in the absence/presence of different ant species in different groups was analysed by Chi-square test. One way ANOVA followed by Tukey's *post hoc* was used to analyse the number of aphids that dropped off the twig in the absence/presence of different ant species in different predator groups. The statistical analysis was performed by SPSS (v. 25).

Results

The percentage of aphids consumed or killed in the presence/absence of the ants in different predator groups varied significantly. Pair-wise comparisons revealed that CE, i.e. the number of aphids killed and consumed was significantly higher in the absence of ants than in presence of *C. compressus* (Chi square test: $\chi^2 = 21.00$, $P < 0.001$, $df = 1$) or *C. subnuda* ($\chi^2 = 24.67$, $P < 0.001$, $df = 1$) in Predator I group. In Predator II group, the number of aphids consumed by the ladybird beetles was lower in the presence of *C. compressus*, as compared to that consumed by the beetles in the

presence of *C. subnuda* ants ($\chi^2 = 21.33$, $P < 0.001$, $df = 1$) and also as compared to that recorded in the absence of both the ant species ($\chi^2 = 16.67$, $P < 0.001$, $df = 1$). The number of aphids preyed upon in case of 'both predators' group was significantly higher in the absence of ants as compared to the number of aphid prey consumed in the presence of *C. compressus* ($\chi^2 = 20.33$, $P < 0.001$, $df = 1$) and *C. subnuda* ($\chi^2 = 26.67$, $P < 0.001$, $df = 1$) ants (Fig. 1A). The NCE was recorded in terms of number of dead aphids found in the Petri dish in each case at the end of the 24 h period in the different groups. There was no significant difference in the percentage of dead aphids in the presence or absence of different ant species in the experimental arena in various treatment groups (Fig. 1B).

The number of aphids that showed 'escape behaviour' by dropping off the twig in different groups, under different conditions varied significantly (Predator I: $F = 7.831$; Predator II = 9.708 ; both predator = 15.057 ; $P < 0.001$ & $df = 2$ in each case). Tukey's *post hoc* test revealed that the number of aphids which dropped off the twig was significantly higher in the absence of ants in 'Predator I', 'Predator II' and 'both predators' categories ($P < 0.001$, in each case) whereas no significant ($F = .346$, $P = 0.708$, $df = 2$) differences were found in the ant-excluded and -included groups of the control (Fig. 2).

Discussion

The results of laboratory experiments clearly demonstrated that the presence of ants in the experimental arena influences the impact of CEs of the spider and ladybird predators on the aphids. Although the generalist predator, *O. javanus* preyed upon the aphids, its predation rate (number of aphids consumed in 24 h) was reduced significantly in presence of the two arboreal foraging, *C. compressus* and *C. subnuda* ants. This reduction in predation rate was more pronounced in the presence of *C. subnuda* ants. The ladybird beetle, *C. transversalis* being a specialist aphid predator did consume more

aphids as compared to the spiders, but the CE of the beetles was also reduced by the presence of *C. compressus* ants and comparatively less number of aphids was used as prey. When these two species of predators were together allowed access to the aphids, they consumed highest per cent of prey under ant-excluded conditions as compared to the two sets of ant-inclusion (each including a single ant species) experiments. Further, the coccinellid showed higher consumption of aphids as prey in the presence of *C. subnuda* as compared to that shown in the *C. compressus* inclusion experiments in predator II category.

Our study shows that the CE of both the spiders as well as the ladybird beetle is negatively impacted by the presence of tending ants in the experimental arena since ant presence promotes the survival of aphids. Apparently the presence of hemipterans alters ant behaviour so that ants become more aggressive and attack insects that they might otherwise ignore, including other predators as well as other (non-honeydew-producing) herbivores (Way, 1963). Often the best protectors are reported to be competitively dominant ant species that exhibited aggressive behaviours towards other arthropods in the community (Grover *et al.*, 2007; Fagundes *et al.*, 2017; Clark and Singer, 2018). Hence, under natural field conditions the presence of ants on the plants may have multiple and/or cascading effects on the host plant and other members of plant-visiting arthropod communities. Thus ants defend aphids as well as the EFN-bearing plants from their enemies but the defence quality has been shown to be important in food-for-protection associations between ants, plants, and hemipterans.

Our study shows that presence of ant influences the defensive, escape behavioural response of *A. gossypii*, when one or both the species of arthropod predators were present in the experimental arena. It is also worth noting that the 'dropping down' behaviour was consistently and significantly higher when aphids were

Fig. 1: A. Consumptive (mediated via predatory activities) and B. non-consumptive effects (mediated via 'fear factors' associated with the presence of predators) of spiders and ladybird beetles on the number (Mean $\pm$ SE) of aphid, *Aphis gossypii*, in different categories of laboratory-based Petri dish experiments: control (both species of predators, *Oxyopes javanus* and *Coccinella transversalis* excluded) and treatment experiments: predator I (including only *O. javanus* spider), predator II (including only ladybird beetle, *C. transversalis*), and both predators (including both, *O. javanus* and *C. transversalis*), each under 3 conditions: (i) excluding both species of ants, *Camponotus compressus* and *Crematogaster subnuda*, (ii) including only *C. compressus*, and (iii) including only *C. subnuda*, studied in a Petri dish arena. Means indicated by different letters within a panel are significantly different from one another (Chi square test, $P < 0.001$).

Fig. 2: Number (Mean $\pm$ SE) of *Aphis gossypii* aphids showing 'escape response' in different categories of laboratory-based Petri dish experiments: control (both species of predators, *Oxyopes javanus* and *Coccinella transversalis* excluded) and treatment experiments: predator I (including only *O. javanus* spider), predator II (including only ladybird beetle, *Co. transversalis*), and both predators (including both, *O. javanus* and *C. transversalis*), each under 3 conditions: i. excluding both species of ants, *Camponotus compressus* and *Crematogaster subnuda* ii. including only *C. compressus*, and iii. including only *C. subnuda*). Means indicated by different letters within a panel are significantly different from one another (One-way ANOVA followed by Tukey's *post hoc* test, $P < 0.001$).

confronted by the aphidophagous ladybird beetles either alone (in predator II group) or along with the generalist spider predator (in 'both predators' group), in the absence of the ant species, as compared to that found in the presence of mutualistically associated ants.

The NCEs (in terms of the number of aphids found dead in the Petri dish at the end of 24 h) of the spiders and the ladybird beetles on the aphids was higher (an exception being predator II group) though not significantly so, in the absence of ants as compared to when ants were present. The non-consumptive effect on the mortality of potential aphid prey, arising from the presence of the two species of predators in the Petri dish arena is plausibly the result of the physiological stress as evident from their escape responses, which were more strongly manifested in the absence of tending ants. The differential effects of spiders and ladybird beetles on the escape responses and NCEs on the cotton aphid found in the present study provides support to earlier studies which report that in predator-prey interactions between aphids and ladybird predators, the aphids withdraw their mouthparts from their feeding site and drop down from the plants (Nelson and Rosenheim, 2006). Further, the species-specific differences in the size and activity of the potential predator, are also known to influence the dropping down behaviour of aphids (Humphreys *et al.*, 2021). They also showed that the ladybird beetles had stronger impact on the dropping down behaviour of pea aphid and potato aphids.

Conclusion

In conclusion, our findings show that honeydew-soliciting, aphid-tending ants play a significant role in providing protection to the sedentary, sap-sucking *A. gossypii* from the CEs and NCEs of both generalist and specialist arthropod predators. Further, keeping in view that the aggressive *C. compressus* and *C. subnuda* ants are also involved in a facultative mutualistic association with the EFN-bearing *C. infortunatum* plants, future research needs to be directed to elucidate the net

effects of these multispecies interactions on the host plant. From a broader perspective, such studies would be of immense significance in the use of natural enemies for the management of the economically important sap-sucking pest, *A. gossypii*.

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