Suicidal Bombing: A Gall Repairing Mechanism in Aphids

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ABSTRACT

Defence colony in eusocial insect is a costly but vital characteristic, whose evolution is modified by kin-selection forces resulting in self-sacrificing behaviour. Social aphids which cause gall reveal an amazing altruism as there are sterile soldiers which take care of defense, cleaning and even repair gall. Natural enemies still occur, but galls have nutritive, protective, and microclimatic perquisites as they are constituted by the secretion of insects and by such plant hormones as auxin and cytokinin. There is division of labour, the younger soldiers take the task of clearing waste and the older soldier's man vulnerable openings. Soldiers in certain species give themselves up by spilling body fluids in order to plug the breakages in the gall. These behaviours point to the adaptation value of gall induction and extreme altruism.

INTRODUCTION

Colony defense is an essential yet risky service of the social insects and the very behaviour of defending the nest gives rise to the untimely death of the defender. Self-sacrificial behaviour are an extreme defence of colonies, they have evolved through kin selection in different social insects. The basis of cooperation and cohesion in eusocial groups is an act known as altruism, and is a behaviour that will reduce direct fitness of the actors to enhance the fitness of a recipient. Members of eusocial groups can easily put their reproductive capacity, food supplies and even their life at stake, in order to do good to their nest mates. These defensive acts are characterized as being similar to other variants of altruism in that they continue to exist in social insects since they work to enhance the fitness of the reproductive members of the colony, which will transfer the genes of the traits of self sacrifice to future generations (Shibao *et al.,* 2021).

1. **Overview of galls**

Galls are the aberrant growths which grow on the leaves, stems, roots or flowers and are induced by insects, mites, fungi, bacteria or nematodes. With insect-induced gall, the insects have a regulatory role on the formation of galls; the gall-shaping stimuli are secreted by the insect in the form of saliva, oviposition fluids, or larval secretions. Production of the plants is of hormonal factors, especially auxins (IAA) and cytokinins, which are regarded as important signals as it causes abnormal cell enlargement and multiplication. Even though the nature of these active substances and the plant pathways they target have not been fully elucidated, plant hormones are the major player. The time of the year when this is very vulnerable is that when the plant tissues are actively dividing that is during late spring but otherwise that is when galls emerge. Gall-making insects tend to be highly host and site-specific and will usually pick not only a certain plant species but also a certain plant part to feed on. Due to their distinctive and differentiated shapes, each gall can usually be used to determine the species of the insect in question, with a given tree often bearing many different species of gall.

Among more than 5100 aphid species, about 80 social species are known from the sub families, that is Hormaphidinae, Eriosomatinae (Blackman and Eastop, 1994) (Table 1).

Table 1. List of gall inducing aphid species and their primary and secondary hosts

Scientific name	Tribe	Primary host	Secondary host
Astegopteryx bambucifoliae	Cerataphidini	*Styrax suberifolia*	Poaceae
Astegopteryx styracicola	Cerataphidini	*Styrax suberifolia*	Zingiberaceae
Ceratoglyphina styracicola	Cerataphidini	*Styrax suberifolia*	Pleioblastus
Ceratovacuna japonica	Cerataphidini	*Styrax japonicus*	Poaceae
Ceratovacuna nekoashi	Cerataphidini	*Styrax japonicus*	*Microstegium spp.*
Ceratovacuna oplismeni	Cerataphidini	*Styrax spp.*	*Microstegium spp.*
Colophina arma	Eriosomatini	*Zelkova serrata*	*Clematis stans*
Colophina clematicola	Eriosomatini	*Zelkova spp.*	*Clematis terniflora*
Colophina clematis	Eriosomatini	*Zelkova serrata*	*Clematis apiifolia*
Nipponaphis distyliicola	Nipponaphidini	*Distylium racemosum*	*Quercus spp.*
Nipponaphis monzeni	Nipponaphidini	*Distylium racemosum*	*Quercus spp*
Tuberaphis styraci	Cerataphidini	*Styrax obassia*	–
Tuberaphis coreana	Cerataphidini	*Styrax formosana*	Loranthaceae
Pemphigus bursarius	Pemphigini	*Populus nigra*	Asteraceae
Pemphigus populitransversus	Pemphigini	*Populus deltoides*	Brassicaceae

Pemphigus protospirae	Pemphigini	*Populus spp.*	Umbelliferae
Pemphigus spyrothecae	Pemphigini	*Populus nigra*	–

2. Life cycle of social aphids

The two soldier making families Pemphigidae and Hormaphididae have very similar life-cycles. The foundress emerges as an egg that is deposited in the body of the primary host on which she develops a gall where she develops parthenogenetically one or more generations of females. Winged aphids abandon the galls typically with midsummer in temperate zones, and fly to the secondary host where they parthenogenetically add wingless aphids. The number of parthenogenetic generations is then created and after autumn colonies form a special winged migrant, called sexuparae, which fly to the primary hosts where they reproduce sexually by giving birth to sexual female and male offspring. These sexuals molted many times and copulated. Every female deposits one egg which overwinters and hatches the following spring, the foundress

3. Colony inner structure of aphid

Division of labour shall be adopted which will enable more efficient use of resources. The adult aphids live inside the gall cavity which in most cases is secure in the upper gallery where the aphids reproduce asexually, In here young Soldier carry out cleaning behaviour by forcing honeydew globules and their shed skin by which colony waste are transferred down to lower gallery. Soldier slowly shift to the lower gall region by replacing the cleaning behavioural pattern into defence because of this constant cleaning behaviour. The Concentration of old soldiers is in lower gall region which is jargoned by the Aphid Colony that is exposed to penetration by the enemies through the waste disposal opening (Shibao *et al*., 2021).

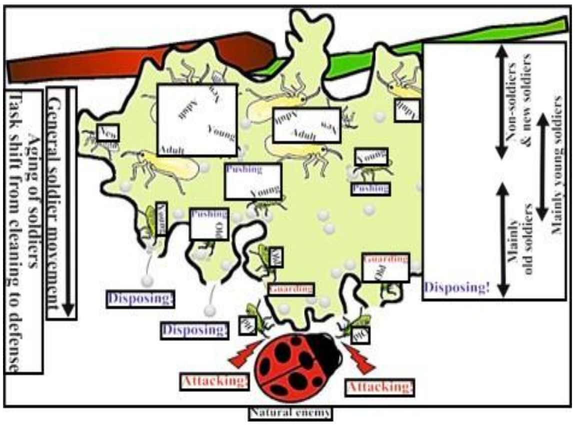

Fig 2. Natural gall colony of *Tuberaphis styraci*, highlighting the relevance of gall structure to production, aging and movement of soldiers

4. Defense in social insects

This is an area in which social insects excel in comparison to other insects, defense. Defense is brought about through major defense compounds, simple defense compounds and minor defense compounds. Suicidal defense or self- sacrificial behaviours may be classified into 3 major groups (Shorter and Rueppell, 2012).

A) Instantaneous defense -The defense results in the death of the defender that entails physically confronting an enemy. Some of these facultative responses are sting autotomy and autothysis. Sting autotomy is the self-amputations of the stinger and poison sac (bees of the genus *Apis,* ants of the genus *Pogonomyrmex*) and self-destruct (also called abdominal dehiscence) is the release of a toxin onto a predator by rupturing the body (carpenter ant, *Camponotus saundersi*).

B) Pre-emptive defense-The suicidal defensive behaviour may occur prior to the actual encounter with a predator by hiding or mending the nest (social aphid, *Nipponaphis monzeni*). **C) Host suicide-**

the altruistic departure or self-removal of ill individuals who abandon the nest to die alone and this reduces the chances of spreading illness to conspecifics (Worker ants of *Temnothorax unifasciatus*).

6. Social behaviour in aphids (Kurosu *et al.*, 2003)

Social behaviour can be termed as joint action among members of the same species. Since aphids reproduce asexually (parthenogenetically) or clonally during most of their life cycle, reproductive altruism within them should be rampant, because members of a clone are genetically identical, any form of altruism with a net cost greater than its benefit should be favoured.

a) **Colony defense** - Colony defense is done by first instar nymph referred to as Soldier. They do not wield their stylet but bear a pair of sharp frontal horns in going after Predators. Seizing two insects with their foreleg and stamping the end of their horns on them. Again and again they strike their bodies forward that horn can enter skin of larvae.

b) **Gall Cleaning** - aphids are sap feeders and produce honeydew which gets sticky and harmful to aphids. Social aphids inhabiting an open-gall with small-Slit on gall-wall young soldier, work by pressing the honeydew globules and their cast skin dew globules, out. Through which colony Waste.

c) **Gall repair** - *N. menzeni* trigger galling on *Distylium racemosum*, a gall is being enlarged and gall wall remains soft, it is then bored into by Lepidopteran larvae. When a hole is made on the gall, it is filled with body fluid, which is glued by the soldiers pressing their cornicles against the hole and the body fluid congealing inside.

7. Hypothesis for the significance of gall induction (Stone and Schonrogge, 2003)

These are some of the hypotheses that have been proposed to explain the adaptive significance of gall induction: three of these relate to discussion of gall morphology:

A. **Nutrition hypothesis-** It involves nutrition of galls that is better than other feeding modes. Gallers with the exception of fungus-feeding gall midges feed on plant tissues or fluids. There is excellent differentiation of nutritive tissues in many galls and these are said to be more nourishing and less defended than non-gall tissues of the same plant and improved nutrition is by wide acknowledgment one of the general benefits of gall induction. It also provide the explanation of diversity in tissues of gall that induce direct contribution to galler nutrition. The best-supported occurrence is of internal tissues in thrips and aphid galls. Each time we find in both groups colonies which numbers thousands of individuals, and which may occupy the gall two or more generations. Her offspring and the founding female feed suctorially on internal gall tissue and the gall characters that increase feeding territory or nutrient food source will be preferable to the selection. An obvious alternative method of increasing the surface area inside the spherical galls is the formation of internal folds, as in some thrips and aphid galls. Proofs of this adaptive modification are given by a recent comparative survey of correlations between gall form and reproduction strategies in galling thrips.

Development of internal folds is associated with the gigantism of the reproductive organs of the founding female (physogastry) and the increased supply is therefore correlated with the increased demand. Division of the gall into a network of radiating hollow spines or into interconnected passageways (both of which exist in aphids) also allows high internal surface area (relative to alternative designs of the same volume). Like other galler lineages such as cynipid gall wasps and most cecidomyiid gall midges, nutritive tissues are confined to discrete larval chambers within other gall tissues that do not appear to serve much in the function of nutritive tissue. There is a great variety in the galls produced by these groups due largely to the non-nutritive tissues involved, and their divergent evolution cannot be simply resolved through the nutrition hypothesis.

B. Microenvironment hypothesis- According to the this hypothesis, gall tissues serve to keep the galler safe against adverse abiotic factors and especially desiccation. Plant-inhabiting gallers growing in the interiors of partially enclosed plants live in the boundary layers of rhizospheres, which are wet to the point of being immersed by fluid and thus are water-stress-buffered as a result. The opinion of gall induction as a selective advantage of the gall in general is universal in the circles of scientists but extremely little is known about the effect on microclimate of differences in morphology. In case the issue of desiccation avoidance played a significant role in gall form evolution, we should find a phenomenon of adaptation to water stress in the galler in xeric environments. What might be met with would be a development of complete closure of the galls where they are only slightly open, or the more or less complete overlaying with layers of waxy or corky tissue, protecting the galler against the accidental opening. It is possible that in high rainfall regions the prevention of flooding has also played a role in gall development. The spoor of a Taiwanese aphid, *Ceratoglyphina styracicola*, has a diaphragm opening on the upper surface. The spine-like structures that begin in the middle of the gall and exit through the opening then spread outwards to make a cauliflower-like shield prevent flooding. The wax laid on the fuzzy outer surface of the gall by individual aphids helps in the shedding of water.

C. Enemy hypothesis- The hypothesis of the enemy argues that galls render gallers immune to attack by natural enemies. In completely enclosed galls any attack has to be mediated by gall tissues, and thereafter modifications of gall morphology that confer increases in galler survival should be selected. Galls provide partial protection against attack by non-specialist predators and pathogens, but are by no means enemy-free space. To find support in general benefit of galling the Enemy hypothesis requires that the condition of gallers, at the time of the origin of galling, had an advantage in lower mortality relative to their non-galling ancestors. This is not possible in well-established galler lineages and we can only do a comparison between extant galling and non-galling taxa. The hypothesis on enemy is supported in the case of galling sawflies whose parasitoids species are few and the mortalities are low compared to the free-living forms. But broader taxonomic sweep in analyses has also revealed that gallers as a trophic group tend to be attacked by more species of parasitoids than characterize free feeding forms. As opposed to the Nutrition and Microenvironment hypotheses, the enemy one, therefore, cannot be favoured as a broad, long-term benefit of gall formation. Given the lethality found in many of the gallers, however, one would expect that there would be considerable selection in order to increase protection.

CONCLUSION:

A very remarkable instance of extreme altruism within the insect world is the suicidal gall repair device of aphids. Sterile soldiers aphids adopt the important role of protecting a colony in some species of aphids. These soldier aphids react to damage of the protective gall a plant structure created by the colony by sacrificing themselves. They produce a unique bodily fluid that dries on being exposed to air, forming a plug that in effect seals the wound in the gall. It is a self-destructive behaviour which is lethally indispensable in ensuring the protection and structural integrity of the colony. This process highlights the evolutionary formation of self-sacrificial features in case of eusocial organism where the groups survival supersedes that of the individual. It epitomizes highly evolved form of collaboration and segregation of duty, such as that found in ants, bees and termites. Remarkably, the wound-healing involved in diet gall repair in the aphid is strikingly similar to wound-healing in higher organisms, e.g. blood clotting in vertebrates, thus a convergent evolution of biological repair strategies. The case, in general, demonstrates how significant is the impact of altruism and collaboration in the development of the complex social systems and shows how sophisticated the assurance of the group survival is by the nature.

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