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# THE POTENTIAL OF VISUAL AND OLFACTORY SIGNALS IN GALL DEFENCE

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**ABSTRACT**

**Avoiding attacks is clearly better than suffering, or even overcoming attacks. Here we discuss the signalling ways by which galls (i.e., gall-inducers) may defend themselves from damage by avoiding attacks. Many colourful galls that are simultaneously chemically and/or physically defended, and/or omit repelling odours fulfilling the general criteria to be tentatively considered as aposematic. It has been shown experimentally that chemically defended galls also emit volatiles that repel relevant herbivores. Thus, both visual and olfactory gall traits may serve as adaptive signals that have been usually overlooked. It is also highly probable that the conspicuous colours (red, yellow) of many galls may also serve physiological functions, such as defence from reactive-oxygen production, from UV, and from excess visible light, or serve other, unknown functions. The certain role of camouflage (especially by being green), in defence from enemies, thus potentially increasing a gall-inducers' fitness, was not given the attention it deserves. Detailed comparative and especially experimental studies on the adaptive role of gall shape, colouration and odours can further shed light on these phenomena.**

**Key words:** Aposematic, camouflage, defence, extended phenotype, galls, herbivory

Galls are abnormal plant growths induced by various insects. Insects induce galls on plant organs such as, leaves, shoots, flowers, and fruits. Galls are not just the typical developmental wound responses of damaged plants, but are rather specialised organs induced by specialised parasites that serve as nurseries for the developing stages of gall- inducing insects, providing a nutrient supply and protection from both abiotic factors (e.g., sun irradiation, wind, dessication, rain and snow), and from natural enemies, such as, pathogens, predators, parasitoids, and non-gall-inducing herbivores (Price et al., 1987; Stone and Schonrogge, 2003; Miller and Raman, 2019; Harris and Pitzschke, 2020; Kurzfeld-Zexer and Inbar, 2021). The gall-inducing habit has evolved independently numerous times among diverse insect lineages, indicating that it has a high adaptive value. Since it seems that the gall-inducing insects control gall induction up to the smallest details, galls are commonly considered their extended phenotype, *sensu* Dawkins (1982). As such, the gall inducing insects control the physiological, anatomical, chemical and visual properties of the gall-bearing plant organ (e.g., Favery et al., 2020). Defensive gall traits against natural enemies are primarily plant-mediated, including chemical and structural traits, and secretion of nectaries that attract mutualistic ants (e.g., Cornell, 1983; Ferreira et al., 2019; Nicholls et al., 2017; Schonrogge et al., 1999). Some gall-inducing insects such as- the Aphidoidea and Phlaeothripidae may actively and aggressively protect galls from natural enemies (Abbot, 2022; Crespi et al., 1997; Inbar, 1998). Galls are typically armed with high levels of defensive secondary metabolites originating in their host-plant metabolism (Rand et al., 2014, 2017; Hall et al., 2017; Martinson et al., 2022). However, some of these defences operate only after enemy attack. Herein, the visual and olfactory defences signals that allow gall-inducing insects in reducing the rate of predation are discussed, an issue that received little attention.

## Defensive signalling

Plant-borne visual and chemical signals are an important component of pollination and seed dispersal by animals, two better studied systems that illuminate the many possibilities and mechanisms of defensive signalling. In this article, the same explanation is used in discussing galls. Aposematic (warning) signalling is a biological phenomenon in which poisonous, dangerous, unpalatable or unprofitable organisms including plants, visually, chemically or vocally advertise these qualities to potentially attacking animals (Ruxton et al., 2004; Lev-Yadun, 2016), as defence from potential enemies. The evolution of aposematic signalling is based on the ability of target enemies to associate signals with the risk, or non-profitable handling, and later to avoid such organisms as prey. In certain instances, there is even an innate tendency to avoid objects with certain colours or colour patterns (Ruxton et al., 2004), a character indicating the long duration of the interactions and the strength of selection. Usually, colours of aposematic plants and animals are yellow, orange, red, purple, black, white, brown, and their combinations (Ruxton et al., 2004; Lev-Yadun, 2001, 2016). Olfactory plant aposematism, whereby poisonous plants deter mammalian or insect herbivores by production of signalling volatiles (e.g., Eisner and Grant, 1981; Massei et al., 2007; Holopainen, 2008; Lev-Yadun et al., 2009; Karban, 2015) is well known. It is possible, that similarly to pollination (Faegri and van der Pijl, 1979) and seed dispersal (van der Pijl, 1982; Schaefer and Ruxton, 2011), where many plants simultaneously use visual and olfactory signals for animal attraction, that such double signalling is also true in diverse instances of plant aposematism. Certain toxic and colourful autumn leaves that could be considered visually aposematic (Lev-Yadun and Gould, 2007; Lev-Yadun, 2022), probably simultaneously use olfactory aposematism to deter various herbivorous insects (Holopainen, 2008).

**The aposematic gall hypothesis**

The general key factors behind the aposematic gall hypothesis, formulated by Inbar et al. (2010a) are:

1. Galls are valuable and irreplaceable asset to their inducers.
2. Because the galls can easily be detected by their natural enemies (invertebrates and vertebrates), and because the gall-inducers cannot actively flee, there is a strong selection for efficient gall defensive traits.
3. Galls are often defended by physical structures and accumulate high levels of chemical defensive compounds compared to intact plant parts.
4. The gall-inducers control gall traits including their colour, shape, chemistry, and volatiles emission.
5. Many galls are visually and/or chemically conspicuous.
6. The colours and scents of plant organs often interact (advertisement) with animals: they attract pollinators, seed dispersers, and deter herbivores.

Visual conspicuousness is a striking and common gall trait. Many galls are visually conspicuous because of their size and shape, which differ from the background of the plant organs that form or carry them. In addition, quite often galls are characterized by bright or contrasting colours such as red and yellow colours (Fig. 1) (e.g., Russo, 2007), as a result of accumulation of plant-derived pigments in their tissues (Czeczuga, 1977), and can be clearly distinguished visually from the surrounding host plant organs. Galls may change colour during their development and aging, especially from green to red, or express such a change in association with exposure to strong sunlight (e.g., Wool, 2004; Isaias et al., 2013). The aposematic gall hypothesis suggests that chemically or otherwise protected galls that are also conspicuous (visually or by odours) are potentially aposematic: warning potential enemies and thus preventing gall destruction before any physical contact and initial damage can be made. The galls, which are made of host plant tissues, are manipulated by their inducing parasites to form both direct defences and signalling. Hence, both the gall-inducing insects and the attacking enemies benefit from this strategy.

The predictions of the aposematic gall hypothesis as proposed by Inbar et al. (2010a) were formulated from several life history traits that are thought to promote aposematism in general *sensu* Mallet and Joron (1999) and Ruxton et al. (2004). Concerning the defence level, chemically and possibly also physically well-defended galls are expected to be usually colourful. Galls that are less well defended, especially from avian predators, will tend to be more visually cryptic. Alternatively, it could be argued that gall's conspicuousness is a defence strategy of the plant to attract potential enemies of the gall-inducing insects. Inbar et al. (2010a) proposed that if the aspect of indirect plant defence by gall colouration, which may attract the gall's enemies is true, less-defended galls should be more colourful and conspicuous to enhance learning of their predators. This explanation awaits deeper examination. They also suggested that the ability to overcome initial and partial damage (gall repair), and thus accelerate enemies' avoidance learning without self scarifying, should promote the evolution of gall aposematism. Many poisonous plants emit characteristic volatiles that may deter herbivores (Eisner and Grant, 1981; Rothschild, 1986; Massei et al., 2007). It is thus expected that well-

Fig. 1. The signalling galls (see Rostás et al 2013) of the aphid *Slavum wertheimae* that induced large (as a tennis ball) galls on *Pistacia atlantica*. (Photo: Moshe Inbar).

defended galls will emit a distinct blend of volatiles that will serve as a warning olfactory signal.

**Conspicuous galls: alternative explanations**

The aposematic gall hypothesis (Inbar et al., 2010a) encouraged researchers to pay attention to the potential adaptive role of gall signals or to propose alternative explanations.

*Gall colouration is related to senescing*: White (2010) argued that a gall's colour is related to the senescing status of the galled tissue. He suggested that dying gall tissues release nutrients to the benefit of the gall inducer. Furthermore, he argued that the gall inducers induce the plant organ to initiate the gall around the gall inducer's feeding action, after the rest of the plant body has stopped growing (White, 2010). However, gall colour has limited association with the senescing state of the galled tissue, and redness can also be seen in young and fast-growing galls (Inbar et al., 2010b). The tissues of young red galls are commonly meristematic and not dying, and when galls grow, the rest of the host plant, and even the immediate gall-bearing organ (e.g., leaf, leaflet) grows as well. One should keep in mind that redness and yellowing are not synonymous with senescence (Inbar et al., 2010b). Many young and growing flowers are red and yellow (Lee, 2007) and many young leaves are red (Richards, 1996; Dominy et al., 2002; Lev-Yadun et al., 2012). Nevertheless, gall colour probably could have evolved along physiological routes such as stress-related colouration or because of pleiotropic effects of defensive genes. Still, White's (2010) hypothesis may theoretically be relevant for at least some gall inducers, but certainly not for all.

There are numerous colourful galls, representing thousands of different gall- inducing species. They represent many repeated but independent events of galling habit evolution. They are found in different environments and on a great variety of plant taxa, host life stages and organs. It is unreasonable to assume that all these galls have only a single and ubiquitous function for their conspicuous colour. Indeed, Inbar et al. (2010a) discussed several alternative explanations for this phenomenon. Moreover, gall conspicuousness and signalling are dependent not only on colour, but also on size and shape (Stone and Schonrogge, 2003) and even on odour (see Rostás et al., 2013). A single physiological explanation, such as the level of light exposure, also cannot explain all the variation in gall colouration, as colourful galls are also common in less illuminated microhabitats (Inbar et al., 2010b).

*Gall colour is a by-product of gall induction*: Connor et al. (2012) argued that the redness of many galls is simply a by-product of the galling process ("a fabricational noise"). They suggested the following line of reasoning: (1) Many gall-inducing bacteria (and some fungi) are known to produce cytokinins, similarly, gall-inducing insects have been found to harbour high levels of cytokinins (Yamaguchi et al., 2012), which may differ from the host plant's cytokinins. (2) Insect-induced galls are mobilization sinks for photosynthates and cytokinins are known to be involved in strengthening mobilization sinks in active plant sinks. (3) Cytokinins and high-sugar concentrations are involved in the production of flavonoids, including anthocyanins, and therefore, the colouration is due to accumulation of anthocyanins as a side-effect of the combination of high sugar and cytokinins. (4) Sugars suppress carotenoid synthesis, suggesting that it is unlikely that the colouration is due to carotenoid accumulation. (5) Connor et al. (2012) referred to White (2010), accepting that reddening is associated with senescence.

In spite of these suggestions, the biology of plants in general and that of galls in particular are not so simple (Gerchman et al., 2013). However, galls may come in many colours: red, yellow, pink, purple, green, brown, and their combinations, and since gall colouration can change, more than one factor determines the evolution and expression of gall colour. Some galls change their colour during their development or when exposed to sunlight (see photos in Russo, 2007; Redfern, 2011), while others redden without being exposed to direct sun light, even when induced on the shaded abaxial side of the leaf. Others, however, will always remain green, both inside and outside. This variation of colours suggests that anthocyanins could be only one of the multiple pigment types involved in gall colouration. For example, many insect-induced galls are yellow (e.g., Russo, 2007). This challenges Connor et al.'s (2012) suggestion that carotenoids are unlikely to be involved in gall pigmentation because sugars suppress the synthesis of carotenoids. Moreover, the fact that there are so many yellow–orange, sweet ripe fruits that change colour from green to yellow or orange, along with a dramatic increase in their sugar content (e.g., mango, apricot, peach, and various date varieties), demonstrate that sugars do not suppress carotenoid synthesis in principle.

Another problem with Connor et al.'s (2012) suggestions is that in addition, anthocyanin and cytokinin levels do not often correlate (Gerchman et al., 2013). Anthocyanins are pigmented flavenoids common in many plant tissues. To date more than 700 anthocyanins have been reported (e.g., Wallace and Giusti, 2015). Anthocyanin content has been found to increase under various conditions, some of which, but definitely not all, and not even the majority, are sink tissues. Elevated levels of anthocyanins were demonstrated in both young expanding and in senescing foliage (Richards, 1996; Dominy et al., 2002; Lev-Yadun et al., 2012), in flowers (Grotewold, 2006), in many ripe fruits (Allan et al., 2008), and as a response to low temperatures (Hughes, 2011). While some of these (namely young expanding leaves) could be considered as sink tissues, others, such as senescing leaves, are source tissues and not sinks. Altogether, the connection between anthocyanin content and high cytokinin levels is far from being deterministic. Young and growing fruits, a definite sink tissue, include high levels of cytokinins, but are green. A similar trend was reported for nitrogen starvation conditions (Close and Beadle, 2003), where anthocyanins accumulate but cytokinin levels do not, and in some instances even decline (e.g., Yong et al., 2000). Young roots, strong cytokinin producers, are usually pale. Finally, some cytokinin-secreting organisms are known to induce 'green islands' on senescing colourful leaves (Walters et al., 2008), which are, as their name implies, green. Altogether, there is no universal trend of cytokinins inducing reddening.

Connor et al. (2012) also pointed out in their opposition to the aposematic gall hypothesis that in a given gall system, insectivorous birds and mammals attack galls in the cold winter months, when galls have lost their redness. This might be true in some systems, but in the Mediterranean habitats, for example, galls induced by the Aphidoidea are attacked by birds in the summer and fall (August-Decmber) (Burstein and Wool, 1992; Inbar personal observations). One could easily adopt a counter explanation to Connor et al.'s (2012) proposal; accordingly, this can be regarded as a suitable example for red (aposematic) colouration's defensive role, i.e., when the galls are red and signal their defence, they are not attacked. Gerchman et al. (2013) concluded that the hypothesis proposed by Connor et al. (2012), although stimulating and possibly even true in certain instances, was an over simplification, in general. Even if the cytokinin byproduct hypothesis *sensu* Connor et al. (2012) is the mechanism of gall reddening in certain taxa, it is not a universal rule, and does not provide a negative proof for other explanations of gall colouration.

Overall, the suggestion that aposematic signalling does not operate in galls (White, 2010; Connor et al.,

2012) referred only to the visual aspect (see Rostás et al., 2013). However, olfactory aposematism seems to operate both independently of, and/or simultaneously with the visual one (e.g., Damasceno et al., 2010; Klimm et al., 2020; Villagra et al., 2021). We stress that as shown in many fungi (e.g., *Amanita* spp) (Sherratt et al., 2005), olfactory aposematism may be especially important as a defence against either colour blind or nocturnal enemies, or within or under dense canopies that are not well illuminated, environments highly appropriate for many gall species. Olfactory aposematism may be especially important for galls as a defence against predatory and parasitic insects and mammalian herbivores. Clearly, gall-inducers can control the olfactory signals of the galls (if needed) to prevent their detection by natural enemies (Tooker et al., 2008). Another alternative explanation for galls being red is that anthocyanins are known to defend leaves and fruits from fungal attacks (Coley and Aide, 1989; Schaefer et al., 2008; Schaefer, 2011; Tellez et al., 2016), and since the internal cavities of many galls are humid, defence from fungal attacks is probably equally relevant for the gall inducing insects as well.

### Testing the aposematic gall hypothesis

Inbar et al. (2010a) proposed several models to test the aposematic gall hypothesis. However, comparative surveys and analyses (within and between species) of gall colouration, their chemical defence levels, and gall position (e.g., shaded *v* directly exposed to the sun) in varying ecosystems are needed. Nevertheless, controlled experiments (field and laboratory) in which accelerated associative learning of relevant enemies, i.e., insect and mammalian herbivores (see Berman and Inbar, 2023), predators (vertebrates and invertebrates) and parasitoids needs to be tested. Additional analyses of the unique volatile emission by the galls and their impact on potential enemies are also needed. Alternatively, proven aversion, be it inherited or of experienced individuals from colourful or odourous galls, can also indicate gall aposematism. Clearly, descriptive, theoretical and experimental data are still needed to evaluate the generality of gall aposematism. Moreover, the possibility of Müllerian and Batesian mimicry should also be considered in defensively signalling galls.

Several studies have considered, but not necessarily supported the aposematic plant gall hypothesis (e.g., Dias et al., 2013; Álvarez, 2012; Patankar et al., 2012; Bomfim et al., 2019; Luz et al., 2015; Miyazaki et al., 2020; Fernandes et al., 2022). So far, only one study (Rostás et al., 2013) experimentally tested the visual aposematic gall hypothesis. The aphid *Slavum wertheimae* (Hemiptera: Fordini) (Fig. 1) induces large and conspicuous, often red, galls on the lateral shoots of *Pistacia atlantica* (Anacardiaceae). The galls included nearly four times higher levels of tannins and nearly two times greater concentration of terpenes compared with non-galled *P. atlantica* leaves **(**Rostás et al., 2013). These galls also emit distinct and higher levels of volatile plant terpenes than the neighbouring leaves. They experimentally showed that goats sensed these emitted volatiles, in particular the combination of α-pinene, sabinene, and limonene as olfactory signals serving as feeding deterrents. As a result, goats consumed all the leaves of *P. atlantica* but most of the galls on the consumed shoots remained intact **(**Rostás et al., 2013).

Whatever be the reason for the evolution of gall colouration, we still have to explain its variability and maintenance. It is widely accepted that gall inducers regulate gall traits (‘extended phenotype’). Thus, if conspicuousness would have had a strong negative effect on gall survival (e.g., by attracting predators and parasitoids) it is expected to impose a strong selection against it (Inbar et al., 2010b). Inbar et al. (2010b) thus explained that the conspicuousness of galls is sound evidence of its potential beneficial role, or at least for the lack of strong selection against it. An interesting example of the sophisticated ability of the inducing insect to control gall signalling trait has been reported by Tooker et al. (2008). They demonstrated that gall-inducing insects can ‘silence’ the emission of conspicuous odour (volatiles) from the gall-bearing organs, which thus reduces its detection by potential odour-oriented enemies.

## CONCLUSIONS

In conclusion, there is potentially strong selection for gall defence from a variety of natural enemies: pathogens, parasitoids, herbivores, and predators, both arthropods and vertebrates (Price et al., 1987; Wool and Burstein, 1991; Schultz, 1992; Zamora and Gómez, 1993; Inbar et al., 2003; van Hezewijk and Roland, 2003; Gerchman and Inbar, 2011; Kurzfeld-Zexer and Inbar, 2021). Many gall traits are influenced by such selection pressures (Price et al., 1987; Stone and Schonrogge, 2003). Gall signalling (colouration, shape, and scent) may be part of their defensive arsenal. Insects can manipulate the chemical production and accumulation of defensive substances in the galls

(Martinson et al., 2022; Davidovich-Rikanati, 2022), alter volatile emission from the galls to reduce the level of parasitism or deter enemies (Tooker et al., 2008; Rostás et al., 2013; Barônio and Oliveira, 2019), and manipulate gall phenotypes including pigmentation (Korgaonkar et al., 2021; see also Maderspacher, 2021). Considering the selective evolutionary forces on the gall systems, and having the ecological, behavioural, biochemical and molecular tools available, the adaptive significance (or not) of gall signalling could be readily addressed, and many new and exiting discoveries are expected.

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