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Why do many galls have conspicuous colors? A new hypothesis

M. Inbar · I. Izhaki · A. Koplovich · I. Lupo · N. Silanikove · T. Glasser · Y. Gerchman · A. Perevolotsky · S. Lev-Yadun

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Abstract Galls are abnormal plant growth induced by various parasitic organisms, mainly insects. They serve as "incubators" for the developing insects in which they gain nutrition and protection from both abiotic factors and natural enemies. Galls are typically armed with high levels of defensive secondary metabolites. Conspicuousness by color, size and shape is a common gall trait. Many galls are colorful (red, yellow etc.) and therefore can be clearly distinguished from the surrounding host plant organs. Here we outlined a new hypothesis, suggesting that chemically protected galls which are also conspicuous are aposematic. We discuss predictions, alternative hypotheses and experimental tests of this hypothesis.

Keywords Aposematism · Chemical defense · Extended phenotype · Plant manipulation · Warning coloration

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M. Inbar (✉) · I. Izhaki · A. Koplovich · I. Lupo
Department of Evolutionary & Environmental Biology, Faculty of Science and Science Education, University of Haifa, Haifa 31905, Israel
e-mail: minbar@research.haifa.ac.il

N. Silanikove · T. Glasser
Institute of Animal Science, Agricultural Research Organization, Bet Dagan 50250, Israel

Y. Gerchman · S. Lev-Yadun
Department of Science Education - Biology, Faculty of Science and Science Education, University of Haifa, Oranim, Tivon 36006, Israel

A. Perevolotsky
Department of Natural Resources, Institute of Field Crops, Agricultural Research Organization, Bet Dagan 50250, Israel

Introduction

Many herbivorous insects induce galls on various plant organs such as leaves, shoots and flowers. Gall-formers manipulate and exploit the development, anatomy, morphology, physiology and chemistry of the host plant (Weis et al. 1988; Shorthouse and Rohfritsch 1992) to their own benefit. Galls, being plant tissues, act as physiological sinks for mobilized plant resources, resulting in increased nutritional values for their inducers. They serve as "incubators" for the developing insects that gain protection from abiotic factors (e.g., sun irradiation, wind, rain and snow) and from natural enemies such as pathogens, predators and parasitoids (Price et al. 1987; Stone and Schonrogge 2003). Because the inducing insects control gall formation up to the smallest details, galls are commonly considered as their extended phenotype (Dawkins 1982; Crespi and Worobey 1998; Stone and Schonrogge 2003; Inbar et al. 2004). An earlier (but less likely) hypothesis, suggested that galls could represent adaptations of the host plants; restricting insect damages to specific organs (see Stone and Schonrogge 2003).

The evolutionary and ecological contexts of many gall traits have been intensively studied (e.g., Stone et al. 2002; Raman et al. 2005). Numerous studies have examined the biochemical composition of gall tissues both from the nutritional and defensive points of view (e.g., Inbar et al. 1995; Nyman and Julkunen-Titto 2000). Defensive gall traits against natural enemies attracted much attention from ecologists and evolutionary biologists (e.g., Cornell 1983; Abrahamson et al. 1989; Schonrogge et al. 1999). For example, the high levels and compartmenting of defensive phenolics and tannins in galls are explained as an adaptive trait that protects the galling insects (Cornell 1983; Hartley 1998).

Conspicuousness is a striking and common gall trait. Many galls may be conspicuous because of their size and shape which is different from the background plant organs. Often, galls are "ornamented" with bright (red, yellow, etc.) colors (e.g., Fig. 1; Russo 2007) as a result of accumulation of plant-derived pigments in their tissue. For example, the red galls of wasps (Cynipidae) induced on oaks contain high levels of carotenoids (Czeczuga 1977).

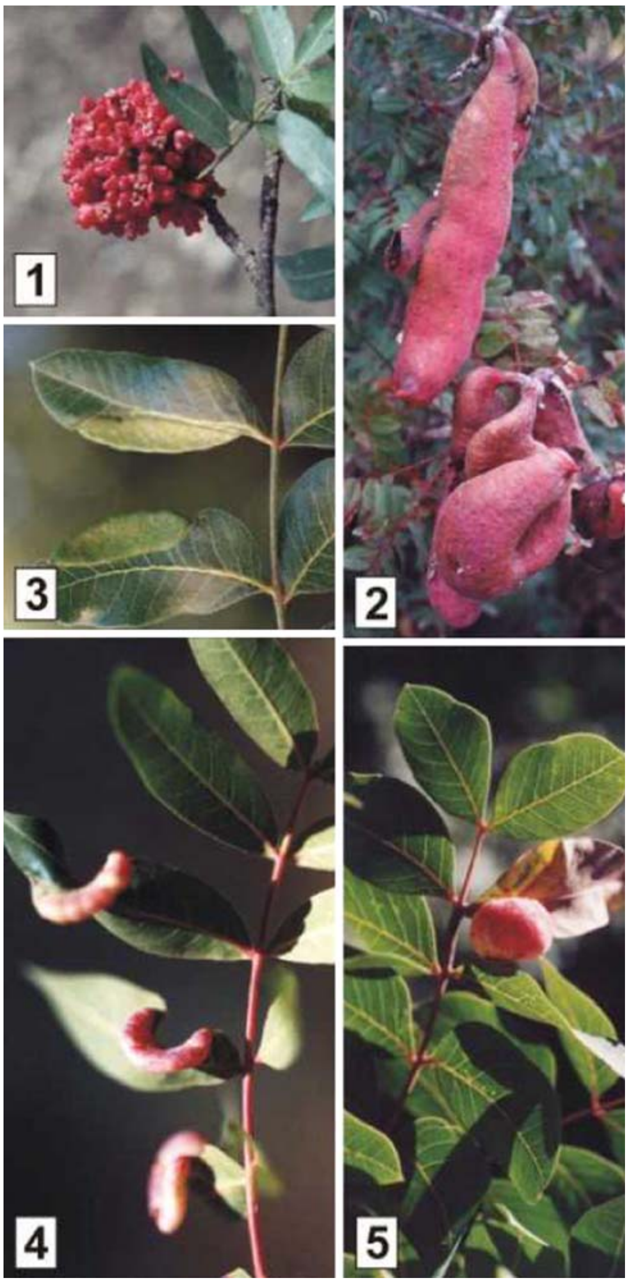

Fig. 1 Aphid galls (Fordinae) on *Pistacia* in the Mediterranean forest. (1) Cauliflower-shaped galls of *Slavum wertheimae* (diameter ~10 cm) on *P. atlantica*. Galls produced on *P. palaestina* (2–5): (2) Banana-like (shape and size) galls of *Baizongia pistaciae* (up to 25 cm long); (3) Green cryptic flat galls of *Paracletus cimiciformis* (2 cm long); (4) Crescent galls of *Forda formicaria* (up to 3 cm long); (5) Spherical galls of *Geoica wertheimae* (~vol 4 cm^3)

Some galls may change color during their development, especially from green to red. Surprisingly, the adaptability, functionality and the evolution of gall conspicuousness have been practically ignored. Only a few studies casually mentioned the nature and putative function of gall coloration. Hence, it has been suggested that the red color of several oak wasp-galls attract parasitoids (Stone et al. 2002 and references therein). Wool (2004) noted that pigmentation in some aphid galls is associated with exposure to light.

Plant coloration (pigmentation) and signaling

Non-green pigmentation (coloration) in plant organs has several physiological roles. Red and yellow pigments provide protection from photoinhibition and photo-oxidation (Close and Beadle 2003). Nevertheless, except for photosynthesis, plant pigments have the potential to serve additional functions concurrently (Gould et al. 2002; Lev-Yadun et al. 2004; Schaefer and Wilkinson 2004; Archetti et al. 2009). It is well accepted that plant pigmentation can serve as attracting signals to animals, especially in relation to pollination and seed dispersal (Willson and Whelan 1990; Schaefer and Schmidt 2004; Chittka and Raine 2006), and attraction of insects to traps of carnivorous plants (Joel et al. 1985; Schaefer and Ruxton 2008).

Aposematic (warning) coloration is a biological phenomenon in which poisonous, dangerous or otherwise unpalatable organisms visually or chemically advertise these qualities to other animals (Cott 1940; Edmunds 1974; Gittleman and Harvey 1980; Ruxton et al. 2004). The evolution of aposematic coloration is based on the ability of potential enemies to associate the visual or olfactory signal (by learning or innate aversions) with the risk, damage, or non-profitable handling, and to avoid such organisms as prey (Chittka and Osorio 2007; Edmunds 1974; Ruxton et al. 2004). Typical colors of aposematic animals are yellow, orange, red, purple, black, white and brown and combinations of these (Cott 1940; Edmunds 1974; Ruxton et al. 2004). Aposematic coloration in plants has received much less attention than in animals. Visual aposematism was proposed to operate in poisonous and colorful plants (e.g., Rothschild 1986), but sometimes dismissed in various types of plant coloration (Knight and Siegfried 1983; Lee et al. 1987). Only recently aposematic coloration in plants received significant attention and recognition. Several studies suggested that the conspicuous coloration of thorns and leaves may honestly advertise unpalatably to herbivores (Lev-Yadun 2001, 2003, 2009; Rubino and McCarthy 2004; Ruxton et al. 2004; Speed and Ruxton 2005; Hill 2006; Archetti et al. 2009, but see Schaefer and Wilkinson 2004; Chittka and Döring 2007).

Olfactory aposematism, whereby poisonous plants deter mammalian or insect herbivores, has been proposed as well (Eisner and Grant 1981; Rothschild 1986; Guilford et al. 1987; Provenza et al. 2000; Massei et al. 2007).

The aposematic gall hypothesis

We propose that galls that exhibit a combination of high levels of defensive compounds (Cornell 1983; Hartley 1998; Nyman and Julkunen-Titto 2000) with conspicuousness—size, shape, bright coloration and possibly odor, are aposematic. The galls, which are made of host plant tissues, are manipulated by the inducing parasites to form all the components of aposematism (chemical defenses and warning coloration or odors). The components of the aposematic phenotype are expressed externally in the gall tissue, protecting the galling insects and not the host plant that produces them, as the hosts have no interest to protect their parasites. Advertisement of chemically-defended galls may reduce predation by mammalian herbivores, avian insectivores and frugivores and various arthropods. Frugivorous vertebrates (birds and mammals) are often attracted or deterred by fruit coloration which is stage dependent (ripe and unripe) (Snow and Snow 1988; Schaefer and Schmidt 2004; Hill 2006; Lev-Yadun et al. 2009). Colorful galls may therefore attract frugivores as ripe fruits. Nevertheless, conspicuousness (advertisements) is context-dependent based on the experience and learning of the receiver and the reward given. Plant shape, position and maybe scent (see below) may enhance the learning process of frugivores and predators and sharpen their discriminative response to colors in the canopy arena.

Tetrachromatic avian predators that can access galls across the canopy are probably among the most important enemies involved in the evolution of gall visual signaling. Primates also efficiently use visual (coloration) cues while feeding on fruits and leaves, whereas the color of the backgrounds is critically important (e.g., Dominy and Lucas 2001; Vogel et al. 2006). Indeed, bird and mammal predation (e.g., Burstein and Wool 1992; Hill et al. 1995), may impose strong pressure on gall traits (e.g., Abrahamson et al. 1989; Zamora and Gómez 1993; Schonrogge et al. 1999). Insects, both predators and parasitoids are thought to be the most important enemies of gall formers (Price et al. 1987; Stone and Schonrogge 2003). Although some insects can see reddish wave lengths (Briscoe and Chittka 2001), most of them may see the galls in gray colors. Red galls therefore would be still much different and distinguishable from the surrounding plant coloration (e.g., green) for the arthropod's eye (see Chittka and Döring 2007). Together with size and shape (and probably characteristic blend of volatiles), galls could therefore provide clear visual and olfactory signals to these important natural enemies. Interestingly, it has been recently demonstrated that the coloration of leaves can effectively serve as a signal for birds. The coloration of lancewood (*Pseudopanax crassifolius*) leaves that changes trough the ontogenesis of the plant served as an defense mechanism (being cryptic vs. aposematic) as the bright tissues of spines on sapling leaves can be readily detect by moas (Fadzly et al. 2009).

The predictions of the aposematic gall hypothesis are developed from several life history traits that are thought to promote aposematism in general (Mallet and Joron 1999; Ruxton et al. 2004):

(1) Defense levels. Only chemically well defended galls are expected to be colorful. Galls that are less well defended (especially from avian predators) will tend to be more cryptic. Alternatively, it could be argued that advertisement of galls is a defense strategy of the host plant to attract potential enemies of the galling insects. If true, we would expect to find more colorful and conspicuousness in less-defended galls to enhance learning of their predators.

(2) Aggregation. Colorful and aposematic galls will be found in species that form aggregated communities. Warning coloration in phytophagous insects (in this case gall-formers) is often associated with gregariousness (Bowers 1993; Hunter 2000). Aggregation should enhance early detection, innate aversions or learning by the predators, thus increasing the effectiveness of the warning signal (Edmunds 1974).

(3) Longevity. Colorful galls will be more common in species with prolonged development and persistence. Long-living aposematic species can promote predators to learn to avoid similar individuals or trait (Blest 1963). Furthermore, aggregations in long lasting and sessile galls should increase the risk of attack if avoidance learning is not involved.

(4) Size and shape. Large galls (as aggregations) or gall with irregular shape can be more easily detected by potential enemies regardless to color. It is therefore expected, that such galls will be more often both well protected and colorful to accelerate the avoidance learning of predators.

(5) Odor. Some plants may use olfactory aposematism; poisonous plants emit characteristic volatiles that may deter herbivores (Atsatt and O'Dowd 1976; Eisner and Grant 1981; Rothschild 1986; Guilford et al. 1987; Provenza et al. 2000; Massei et al. 2007). We expect that chemically-well-defended-galls will tend to produce characteristic odors.

(6) Ability to tolerate partial damage. The ability to overcome initial and partial damage (gall repair), and

thus accelerate enemy's learning without self sacrificing should promote the evolution of aposematism. We therefore predict that the evolution of gall aposematism should be favored by galls with such ability.

Alternative explanation of gall coloration

Plant pigmentation may have multiple functions (Gould et al. 2002; Lev-Yadun et al. 2004; Schaefer and Wilkinson 2004; Lev-Yadun and Gould 2007; Archetti et al. 2009). Thus, alternative hypotheses concerning coloration of galls need not contrast or exclude any other functional explanation of gall coloration as they may have more than one function. The evolution of gall coloration may reflect an adaptation both to physiological pressures and defensive signaling. Indeed in many gall taxa pigmentation is not a fixed trait and notable polymorphism can be observed.

In some species, gall pigmentation is positively associated with increased light exposure (e.g., Wool 2004), indicating a possible role in protection from the negative physiological effects of excess light (e.g., Gould et al. 2002; Close and Beadle 2003), whereas anthocyanins may have accumulated as anti oxidants. If so, we would expect to find colorful galls only in upper canopy or on the adaxial (upper) side of the leaves that are more exposed to light than galls located on shaded plant parts or shaded habitats such as understory. The aposematic hypothesis will be rejected if gall coloration will be only dependent on the levels of light exposure. However, many gall species always have their typical bright coloration (e.g., Czeczuga 1977) regardless to light exposure.

It is possible that aposematism in galls developed as "side benefit" of multiple protective functions provided by plant pigments (i.e., anthocyanins and carotenoids). Schaefer and Rolshausen (2006) suggested that the main reason for color pigments accumulation in plants is physiological stresses, an explanation that cannot be true in the many cases when advertisement is essential (e.g., animal-pollinated flowers, animal-dispersed fruits). They also suggested a pleiotropic mechanism which is more probable; pigments and many defensive compounds share common biosynthesis pathways. For example, red pigments may be correlated with some defensive compounds that plants use against biotic and abiotic agents (including herbivores). Anthocyanins are derived from the phenyl-propanoid pathway which may also produce tannins and flavonoids. The production of the pigments may therefore correlate (and reliably indicate) higher level of chemical defenses. The defense indication hypothesis (Schaefer and Rolshausen 2006) provides a physiological explanation for the developments of aposematic galls via pleiotropic effects rather than the direct signaling. As mentioned above, if indeed gall pigmentation has a primarily physiological role (e.g., protection from photoinhibition and photo-oxidation) we would expect that galls exposed to solar radiation are more colorful than galls on shaded plant parts. Support for the pleiotropic explanation would be an abundance of colorful but weakly-defended galls; whereas pigmentation could not be linked to signaling but rather to biochemical cascades.

Testing the aposematic gall hypothesis

Several approaches can be used to test the aposematic gall hypothesis. Comparative survey and analyses (within and between species) of gall coloration, chemical defense level and gall position (e.g., shaded vs. exposure to the sun) in several systems is clearly needed. Nevertheless, only controlled experimentations (field and laboratory) in which accelerate associative learning of relevant enemies, preferably herbivores or insectivores, mammals and especially birds will be evaluated can critically test the aposematic gall hypothesis. Learning curves and choice experiments between different galls and between manipulated (painted) gall coloration could be usefully used. As pointed out by Chittka and Döring (2007) coloration of galls should be examined through the eyes (visual abilities) of the potential natural enemies of a given gall former, and the relevant natural background (see also (Sumner and Mollon 2000; Vogel et al. 2006). In cases where gall coloration is variable, manipulation of light exposure and measuring its effect on gall phenotype (color), chemical defense and predator attacks, can distinguish between the aposematic and alternative hypotheses. We also recommend analyses of odors emitted from galls and their correlation with coloration, size, chemical defenses and levels of attack.

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