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Conspicuous gall colors: a response to T. C. R. White

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White (2010) commented on our hypothesis about aposematic galls (Inbar et al. 2010) and we are pleased for the opportunity to further discuss this still enigmatic, common, though variable phenomenon of conspicuous (mainly colorful) galls. White proposed an explanation for gall coloration based on the assumed senescing status of the galled tissue.

Although the feasibility and generality White's physiological/nutritional hypothesis deserves a separate, thorough discussion, one should keep in mind that red and yellow pigmentation is not synonymous with senescence. Many young flowers are red and yellow (Lee 2007) and many young leaves are red (Richards 1996). Galls do not necessarily senesce earlier or stop the development of the galled tissue. As posited in our paper, we can clearly accept that gall coloration could have evolved along physiological routes such as stress-related pigmentation, or pleiotropic effects of defensive genes. As such, White's hypothesis may be relevant for at least some gall-formers.

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There are numerous gall species, of which probably thousands are colorful. They represent many repeated but independent events of evolution of the galling habit. They are found in different environments and on a great variety of plant taxa, host life stages and organs. It is not reasonable to assume that all these galls have only a single and ubiquitous function for their conspicuous coloration. Indeed, in our paper (Inbar et al. 2010) we discussed several alternative explanations for this phenomenon. Moreover, gall conspicuity and signaling is not dependent only on colors, but also on size, shape (e.g., Fig. 1) and probably odor. A single explanation, such as the level of light exposure for example, cannot explain the variation in gall coloration as colorful galls are also common in dark microhabitats (Lupo, Izhaki and Inbar, in preparation).

Whatever the reasons for the evolution of gall coloration, it is still necessary to explain its variability and maintenance. It is widely accepted that gall formers control gall traits ("extended phenotype"). Thus, if conspicuity would have a strong negative effect on gall survival (e.g., by attracting predators and parasitoids) we would expect a strong selection against it. The common conspicuousness of galls is evident for its potential beneficial role; or at least for lack of strong selection against it. An interesting example of the sophisticated ability of gall-inducers has recently been reported by Tooker et al. (2008). They demonstrated that gall-forming insects can "silence" the emission of conspicuous odor (volatiles) from the galled tissue, which thus reduces its detection by potential enemies.

As stated in White's comment, signaling of gall coloration is indeed reasonable; the aposematic gall hypothesis should therefore be considered as a legitimate working hypothesis that awaits proper examination.

Fig. 1 Conspicuous (shape, size, color) gall induced by the aphid *Asiphonella dactylonii* on *Pistacia palaestina*

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