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Position paper.
Ergot (*Claviceps purpurea*) – An aposematic fungus

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Abstract

Predators learn to associate conspicuous signals, such as bright colors, with unpalatability or danger. This defensive strategy is termed Aposematism. We propose that the very poisonous purple-black sclerotia of the infamous fungus *Claviceps purpurea* (ergot) and many other *Claviceps* species are aposematic. Very toxic fungal sclerotia are associated with conspicuous colors (black, yellow, purple, reddish, brown, violet, white and their combinations) and severely harm herbivores that consume the infected plants, thus meeting the criteria for aposematism. Fungi, that only moderately reduce the reproductive capacity of their hosts can protect the host plants from herbivory and weaken the evolutionary tendency of their hosts to evolve better resistance to infection.

Keywords: Aposematic coloration, *Claviceps*, defense, ergot, herbivory, mutualism

1. Introduction

Aposematic coloration is a well known and widespread defensive phenomenon found across the animal kingdom and in many vascular plants. Aposematism is the phenomenon evolved by organisms that are unpalatable or dangerous to potential predators/herbivores, whereby they advertise their bad quality as a food source by a variety of colors, mainly bright and/or contrasting, e.g., red, orange, yellow, black, white, and their combinations (e.g., Cott, 1940; Edmunds, 1974; Gittleman and Harvey, 1980; Lev-Yadun, 2001, 2006; Lev-Yadun and Ne`eman, 2004, 2006; Ruxton et al., 2004) or by odor (Eisner and Grant, 1981). This facilitates associative learning that reduces further use. The vast majority of studies on animal aposematism associate warning coloration with chemical defense (e.g., Edmunds, 1974; Gittleman and Harvey, 1980; Harvey and Paxton, 1981; Ruxton et al., 2004). The common aposematism of spiny animals received much less attention (Cott, 1940; Ruxton et al., 2004; Inbar and Lev-Yadun, 2005; Speed and Ruxton, 2005). In plants, most attention with respect to aposematic coloration has focused on its association with mechanical defense by thorns (Lev-Yadun, 2001, 2003a,b, 2006; Lev-Yadun and Ne`eman, 2004, 2006; Rubino and McCarthy, 2004; Ruxton et al., 2004; Halpern et al., 2007) although certain poisonous plants have been considered as aposematic (Cook et al., 1971; Hinton, 1973; Wiens, 1978; Harborne, 1982; Lev-Yadun and Ne`eman, 2004; Lev-Yadun, 2006). That mushrooms are also aposematic has been hypothesized, however, while some poisonous mushrooms are colorful, many edible ones are similarly colorful. For this reason, the idea of aposematic coloration in fungi (Camazine, 1983) has not been supported as a general phenomenon by field data and taxonomic analysis (Guevara and Dirzo, 1999; Sherratt et al., 2005). Taste and odor seem to be more important as a common aposematic signals in large fungi, probably since many of the animals that usually consume them are nocturnal and because low level of illumination on the forest floor would reduce the effectiveness of bright coloration as a warning signal (Camazine, 1983, 1985; Guevara and Dirzo, 1999; Sherratt et al., 2005).

2. Ergot

Ergot, a fungal disease of rye and other cereals, caused by

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the fungus *Claviceps purpurea*, is one of the most notorious fungi in human history (Matossian, 1989; Bennett and Bentley, 1999; Alm, 2003). There are more than 40 species in the genus *Claviceps* (Pažoutová and Parbery, 1999) which attack grasses, rushes, and sedges. Most ergot species have colorful and conspicuous sclerotia that form on the ears of their host (Tenberge, 1999). Ergot sclerotia develop in only some of the flowers of their host, allowing the infected plants to produce a considerable number of viable seeds. The fungal sclerotia, are rich in a wide array of highly poisonous alkaloids (Mantle, 1969; Lorenz, 1979; Matossian, 1989; van Dongen and de Groot, 1995). Ergotism, the toxic condition in humans and animals that eat *Claviceps*-infected grain, is often accompanied by psychotic delusions, nervous spasms, abortion, convulsions, gangrene, and even death (Mantle, 1969; Lorenz, 1979; Matossian, 1989; van Dongen and de Groot, 1995). The best-known species, *C. purpurea*, forms conspicuous purple-black sclerotia up to several-cm-long on the ears of rye, where they are easily seen. When infected rye (a staple for humans in European countries with cold wet climates) was ground and used to produce bread, non-lethal levels of ergot poisoning caused severe hallucinations or intense burning pain (St Anthony's Fire) and gangrene of feet, hands, and whole limbs, due to the vasoconstrictive action of the ergot alkaloids (De Costa, 2002). Historically, ergotism has killed many thousands of people. For instance, over 40,000 deaths attributed to ergot poisoning were recorded in France in 943 (Prescott et al., 2005). Many witch-trials, and subsequent executions, in medieval Europe over centuries, and possibly some in North America involved women who did not behave according to acceptable norms, most likely as a result of intoxication by ergot alkaloids (Matossian, 1989; Alm, 2003). The pharmacological activities of the fungus are due to components that include lysergic acid diethylamide (LSD) (Matossian, 1989; Bennett and Bentley, 1999; Alm, 2003; Eadie, 2004). People learned to refrain from eating infected rye, and it is likely that herbivores that consume grasses would learn to avoid it too. The antiherbivory functions of ergot alkaloids, against both invertebrates and vertebrates, have led to it being regarded as mutualism: the plants are defended from herbivory by the poisonous substances of the fungi, while the fungi receive nutrition from the host (Clay, 1988).

3. Discussion

We propose that the very poisonous and colorful sclerotia of *Claviceps* species are aposematic. Sclerotia of *Claviceps hirtella* are yellow, those of *C. glabra* brown, those of *C. viridis* green, and those of *C. purpurea* dark purple or black (Lorenz, 1979) – typical colors of poisonous aposematic organisms. Pažoutová (2006) provides detailed data on the colors of sclerotia for most *Claviceps* species on this website. Eighteen species have black or blackish sclerotia, in eight the sclerotia are of various shades of brown, in seven they are yellow, four have red or purple sclerotia, one has green, and one is partly white. Thus, the majority of the *Claviceps* species have conspicuous sclerotia which are also poisonous. The association of unpalatable, very toxic fungal organs (sclerotia) with conspicuous colors (black, yellow, purple, reddish, brown, violet, white, and their combinations), and the well-documented toxicity to herbivores that consume them, meet the criteria for characterizing the association between *Claviceps* and grasses as operative aposematism. Poisonous mollusks, insects or reptiles with bright colors are considered aposematic without experimental data concerning deterrence of their predators. The same should apply when fungi are discussed.

As for the question do large herbivores (sheep, goat, dear, cattle, etc.) pay attention to patterns of plant coloration at the size of ergot sclerotia, the answer is yes. A field experiment, by Cahn and Harper (1976), showed clearly that rumen-fistulated sheep, which could be directly sampled for diet-content, preferred unmarked leaves of *Trifolium repens* over marked (variegated) ones, indicating the probable defensive value of such variegation. Ergot infests cereals which grow in open habitats where grazers usually feed during daytime, optimal conditions for visual aposematism. The function of bright fungal colors deserves more attention. In plants for instance, various pigments may simultaneously serve defense, physiological functions and attraction of pollinators or seed dispersers (Gould, 2004; Lev-Yadun et al., 2002, 2004; Schaefer and Wilkinson, 2004; Lev-Yadun, 2006) and fungal coloration may similarly have more than one function.

The plant/*Claviceps* interactions may be viewed simply as a disease, or as a mutualistic relationship. Defensive mutualism between plants and fungi is well known (Clay, 1988; Bush et al., 1997; Omacinl et al., 2001; Clay and Schardl, 2002), but has not been discussed as an aposematic effect. Fungal endophytes in the genus *Neotyphodium* (Ascomycetes: Clavicipitaceae) form mutualistic associations with a variety of grasses (Clay, 1990; Breen, 1994). The fungal hyphae grow intercellularly in leaf and stem tissues, causing infections that are transmitted exclusively through the seeds of the host plant. The fungus benefits from access to plant nutrient and photosynthetic resources, while the plant benefits from enhanced resistance to insect herbivores or vertebrate grazers (Clay, 1990; Breen, 1994; Elmi and West, 1995). A series of fungal endophyte-mediated-alkaloids provides the basis for the acquired chemical defense against herbivory (Porter, 1994; Justus et al., 1997). Ergot fungi parasitize rye and other grasses, reducing their reproduction, the very poisonous fungus harming the herbivores that eat the infected plants. Potentially, this benefits individual plants, and probably nearby plants too.

The overall gain to the host seems to more than compensate for the moderate reduction in its reproduction.

Since *Claviceps* species need plant hosts, the more toxic the ergots are to herbivores, the better for both ergot and host. Chemicals in the sclerotia may also directly prevent their consumption by the herbivores or from attacks by other fungi and microorganisms. Indeed, large herbivores usually learn to avoid toxic plants (e.g., Howe and Westley, 1988; Lev-Yadun and Ne`eman, 2004), resulting in a reduced tendency to consume infected hosts. For instance, Opossums (*Didelphis virginiana*), are known to develop an aversion towards the very poisonous mushroom *Amanita muscaria*, in part due to the toxin muscimol (Camazine, 1983). Alternatively, ergot fungi may induce abortions or kill the animals that eat ergot-infested species, decreasing grazing pressure. Since low levels of ergot consumption are not lethal, but cause sickness (Clay, 1988; Matossian, 1989), conditions are appropriate for the development of food aversion towards ergot-infected grasses. The array of alkaloids in ergots makes it difficult for herbivores to evolve resistance to ergot toxicity. When ergot fungi protect their host populations against herbivory, they protect their own habitat and benefiting the host plants. They also reduce the host's evolutionary tendency to enhance its resistance to the disease. In our view the association between *Claviceps* and grasses is a fine-tuned ecological tactic that fits the definition of "dangerous liaisons" sensu van Baalen and Jansen (2001). We propose that odor, in addition to color, might be involved in the aposematic signaling of ergots even in their open, well-illuminated habitats as was found for fungi that grow in dark habitats as described by Camazine (1983, 1985), Guevara and Dirzo (1999) and Sherratt et al. (2005).

The hypothesis we present here may apply only to the fungus *Claviceps* that form ergots, or have a broader scope. There are indications for the latter since other fungal taxa express potential aposematic coloration. For example, *Aspergillus* species produce aflatoxin, a fungal metabolite which is a very potent toxin if consumed by animals (Payne and Brown, 1998) and have toxic pigmented sclerotia (black in *A. flavus* and *A. tamarii*) (Raper and Fennell, 1965; Goto et al., 1996; Chang et al., 2001). A similar picture emerges in the genus *Fusarium* (e.g., Toussoun and Nelson, 1968; Bottalico, 1998), as various animals are repulsed by food contaminated with its toxins (Mirocha et al., 1976). Finally, the insect pathogenic fungus *Cordyceps* produces several types of pigments some of which are bright red (Unagul et al., 2005) and seems to fit into the general picture of toxicity associated with bright or contrasting coloration. The lack of an explanation for the association of toxicity with coloration in fungi, is just one reason why these fungi are worthy of further study. We hope that our hypothesis will stimulate observational and experimental research on this overlooked aspect in fungal biology.

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