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Aposematic (warning) Coloration Associated with Thorns in Higher Plants

SIMCHA LEV-YADUN*

Department of Biology, Faculty of Science and Science Education, University of Haifa—Oranim, Tivon 36006, *Israel*

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Aposematic coloration, a well-known phenomenon in animals, has been given little attention in plants. Here I discuss two types of conspicuousness of thorns which are typical of many plant species: (1) colorful thorns, and (2) white spots, or white and colorful stripes, associated with thorns in leaves and stems. Both types of aposematic coloration predominate the spine system of taxa rich with spiny species—Cacti, the genera *Agave*, *Aloe* and *Euphorbia*. The phenomena have been recorded here in over a thousand species originating in several continents of both the Old and New World. I propose that this is a case of vegetal aposematic coloration analogous to such coloration of poisonous animals, and which communicates between plants and herbivores.

Introduction

Aposematic coloration, a well-known phenomenon in animals, has been given little attention in plants. Often a brightly-colored (orange, yellow or white with black markings) animal is dangerous or unpalatable to predators—a trait that confers a selective advantage because predators learn to associate the coloration with unpleasant qualities (Cott, 1957; Gittleman & Harvey, 1980; Harvey & Paxton, 1981; Wiklund & Järvi, 1982). Visual signals are used by many plants to communicate with and advertise to animals. Although the involvement of such signals in pollination and seed dispersal has been shown, a role for conspicuous thorns in plants has not been previously reported. Several authors (Hinton, 1973; Harper, 1977; Wiens, 1978; Rothschild, 1980; Williamson, 1982; Knight & Siegfried, 1983; Smith, 1986; Lee *et al*., 1987; Givnish, 1990; Archetti, 2000) briefly mentioned a possible association between plant bright colors and toxicity, but the scope and significance of this phenomenon was not determined. In fact, aposematic coloration was discounted in some of these studies (Knight & Siegfried, 1983; Smith, 1986; Lee *et al*., 1987). Olfactory aposematism in poisonous plants was also proposed (Eisner & Grant, 1981; Launchbaugh & Provenza, 1993). Only once, Cahn & Harper (1976) showed that rumen-fistulated sheep, which could be directly sampled for diet-content, clearly preferred unmarked leaves of *Trifolium repens* over marked ones.

Thorns provide mechanical protection against herbivory (Janzen & Martin, 1982; Janzen, 1986; Myers & Bazely, 1991; Grubb, 1992) because they can wound mouths, digestive systems (Janzen & Martin, 1982; Janzen, 1986), and other body parts of herbivores. Thus, once herbivores learn to identify thorns they can avoid harmful plants displaying them. The role for conspicuous thorns

*E-mail: levyadun@research.haifa.ac.il

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in plants and their ecological significance has not been previously reported.

Here I describe two types of conspicuousness of thorns that are typical of more than a thousand thorny plant species growing in both the Old and New World (belonging to the taxa Cactaceae, *Agave*, *Aloe* and *Euphorbia*): (1) colorful thorns, and (2) white spots, white stripes or colorful stripes that are associated with thorns in leaves and stems. I propose that both conspicuousness types function as aposematic coloration and signal herbivores about the thorniness of plants, thus protecting them.

Methods

The type, color and markings associated with thorns were examined in four well-known thorny taxa: Cactaceae, *Agave*, *Aloe* and *Euphorbia*. The basic phenomenon was examined in several collections of thorny taxa growing in Isreal. When it was clear that this is a general phenomena, detailed data were compiled by analysing the pictures and text of published monographs on these taxa (Reynolds, 1969; Benson, 1982; Gentry, 1982; Preston-Mafham & Preston-Mafham, 1994; Sajeva & Costanzo, 1994). For *Agave*, the color of thorns was assigned according to the major color, since only a few species have thorns of more than one color. Since cacti have two classes of thorns (spines and glochids), and their thorns have several colors, the color of their spines and glochids was assigned separately.

Results

Colorful thorn systems, many of which are multi-colored, are found in many species of the Cactaceae (Figs 1–4). Usually, the thorns were brown, yellow, red, white, gray, pink, black and tan (Benson, 1982). Benson (1982), listed 174 cacti species, 140 (80.5%) of which have colored spines and 59 (33.9%) colored glochids. Eight species (4.6%) had one color in the spines, 39 (22.4%) two colors, 48 (27.6%) three colors, 24 (13.8%) four colors, 14 (8%) five colors, five (2.9%) six colors and two (1.1%) seven colors. In 13 (7.5%) species the glochids were brown, seven (4%) species red, 28 (16.1%) yellow, ten (5.7%) tan and one (0.6%) gray (Benson, 1982). Preston-Mafham & Preston-Mafham (1994) had pictures of 973 species, 862 (88.6%) of which had white markings associated with the thorns and six (0.6%) species had brown/black markings. Often thorns are made more conspicuous by colorful or white stripes. White markings associated with thorns are very common in the Cactaceae. They are comprised of white wool or felt, and deteriorate with time. Usually, they appear in the upper parts of the plant and are restricted to areoles where they form well-arranged white spots or short stripes. In few cacti species this marking is brown or black (Preston-Mafham & Preston-Mafham, 1994) (Figs 5 and 6). The less colorful ones were not mentioned, but examination of cacti collections indicated that they are usually grayish but never green.

Agave species can have two types of thorns in their leaves: spines at the distal end, or teeth along the margins. In addition to teeth along the margins, many *Agave* species also have stripes along the margins that enhance spine and teeth visibility (Gentry, 1982). The spines and the teeth along the margins of the leaves were either brown (Fig. 7) reddish, gray, black, white or yellow (Gentry, 1982). Gentry (1982), listed 194 *Agave* species, 112 (57.7%) of which have apical thorns, 86 (44.3%) thorns along the margins and 47 (24.2%) species have stripes along the margins (Fig. 8).

In *Aloe* species the colorful thorns are white, red, black or yellow (Fig. 9). Many *Aloe* species have white markings (Fig. 10) and many species have both colorful thorns and white markings (Reynolds, 1969). Reynolds (1969), listed 137 *Aloe* species, 133 (97.1%) of which have thorns along the margins. 94 (68.6%) species have colored thorns, 37 (27%) species have white thorns along the margins, 13 (9.5%) species have white thorns along the margins but no white spots on the leaf surface, 50 (36.5%) species have both white spots on the leaf surface and colored thorns along the margins, three (2.2%) species have white spots on leaf surface but no thorns, 42 (30.7%) species have colored thorns along the margins but no white spots, and two (1.5%) species have both colored thorns along the margins and colored spots (Reynolds, 1969).

In *Euphorbia* colorful thorns and white or whitish variegation or white markings associated

with thorns (Sajeva & Costanzo, 1994) are also common (Fig. 11). Sajeva & Costanzo (1994), listed 80 *Euphorbia* species, 48 (60%) of which have colored thorns. 13 (16.3%) species have white markings associated with thorns along the margins and nine (11.3%) other species have markings of other colors associated with thorns along the margins (Fig. 12) (Sajeva & Costanzo, 1994).

Discussion

Since the coloration and markings of thorns in plants are so wide-spread, it is probably not a neutral or random phenomena. I propose that, similar to aposematic coloration of animals, conspicuousness of thorns is of adaptive value.

Conspicuous thorns are proposed here to be beneficial for plants since herbivorous animals will remember the signal, and tend to avoid subsequent tasting of such marked plants. If the cost of producing and maintaining the signal is lower than the cost of damage it prevents, the gain will be large enough to favor selection for such mutations (Johnstone, 1995). Both annual and perennial plants usually survive damage caused by herbivores (Crawley, 1983), so an herbivore reacting to aposematic coloration is of direct benefit to the individual plant, which will suffer fewer repeated attacks. Hence, as with animals (Sillén-Tullberg & Bryant, 1983), there is no need to propose kin/group selection, or altruism, as the evolutionary drive for the spread of this character. Furthermore, an herbivore might pass over an aposematic individual and eat its non-aposematic neighbor, thus, reducing the competition between the aposematic and neighboring plants.

Production of colorful thorns and white or colorful markings does require resources. However, when a conspicuous aposematic tissue serves more than one purpose, the relative cost of advertisement is reduced. For instance, in certain cacti, the white wool or felt (which mark spine groups) also reduces diurnal temperature extremes, thus protecting the apex (Nobel, 1978). Whether the aposematic signalling is honest is important for evaluating the evolutionary consequences of conspicuous thorns. Evaluating honesty in biological signalling is complicated, especially here since some other colorful or white plant parts are also used for non-aposematic signalling, e.g. signalling of pollinators and frugivores or for reduction of plant temperature. Hence, the colors of plants not only can signify that a plant is spiny, but rather can also "pay attention". The honesty of the aposematic signal is maintained by herbivores that taste the plants. If mimics are overly abundant, the signal loses its deterrent quality because herbivores learn that it is unreliable (Dafni, 1984).

Since aposematic signals associated with thorns appear in plants of diverse geographical and taxonomic origin, I propose that this is an ancient signal that has been selected for many times. This phenomenon, described here in over a thousand species, seems to be used by plants to advertise their defensive ability, and thus to deter herbivores. Many herbivores see colors but a discussion of herbivore vision is not in the scope of this study.

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FIGS. 1–12. (1) Yellow glochids on *Opuntia microdasys* (Cactaceae). (2) Red glochids on *Opuntia* sp. (Cactaceae). (3) Yellow spines on *Echinocactus grusonii* (Cactaceae). (4) Red spines on *Ferocactus pilosus* (Cactaceae). (5) White marking associated with thorns in *Notocactus* sp. (Cactaceae) made of white wool or felt. (6) White marking forming well-arranged white stripes associated with thorns in *Notocactus magnificus*. (7) A brown terminal thorn on a leaf of *Agave sisalana* (Amaryllidaceae). (8) White stripes along the margins of leaves that enhance the visibility of the white thorns in *Agave horrida*. (9) Red teeth along the margins of a leaf of *Aloe ferox* (Liliaceae). (10) White markings on the leaf of *Aloe saponaria* (Liliaceae). (11) Red thorns on *Euphorbia enopla* (Euphorbiaceae). (12) White stripes along the margins of stem ribs that enhance the visibility of the white thorns in *Euphorbia* sp.