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Short Communication

# Müllerian mimicry in aposematic spiny plants

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**Müllerian mimicry is common in aposematic animals but till recently, like other aspects of plant aposematism was almost unknown. Many thorny, spiny and prickly plants are considered aposematic because their sharp defensive structures are colorful and conspicuous. Many of these spiny plant species (e.g., cacti and *Agave* in North American deserts; *Aloe*, *Euphorbia* and acacias with white thorns in Africa; spiny plants in Ohio; and spiny members of the Asteraceae in the Mediterranean basin) have overlapping territories, and also similar patterns of conspicuous coloration, and suffer from the evolutionary pressure of grazing by the same large herbivores. I propose that many of these species form Müllerian mimicry rings.**

Aposematic (warning) coloration is a biological phenomenon in which poisonous, dangerous or otherwise unpalatable organisms visually advertise these qualities to other animals. The evolution of aposematic coloration is based on the ability of target enemies to associate the visual signal with the risk, damage or non-profitable handling, and later to avoid such organisms as prey. Typical colors of aposematic animals are yellow, orange, red, purple, black, white or brown and combinations of these.[1-5] Many thorny, spiny and prickly plant species were proposed to be aposematic because their sharp defensive structures are usually colorful (yellow, orange, red, brown, black, white) and/or associated with similar conspicuous coloration.[5-22] Animal spines also have similar conspicuous coloration and were proposed to be aposematic.[1,5,17,23]

Several authors have proposed that mimicry of various types helps in plant defense, e.g.,[9,24-34] More specifically, Müllerian mimicry was already proposed to exist in several defensive plant signaling systems. The first was for several spiny species with white-variegated leaves.[8,10] The second was for some tree species with red or yellow poisonous autumn leaves.[35] The third cases are of a mixture of Müllerian and Batesian mimicry, of thorn automimicry found in many *Agave* species.[8]

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Here I propose that many species of visually aposematic spiny plants of the following taxa: (1) Cactaceae, (2) the genus *Agave*, (3) the genus *Aloe*, (4) African thorny members of the genus *Euphorbia*, (5) African acacias with white thorns, (6) spiny vascular plants of southeastern Ohio, (7) spiny Near Eastern plants with white variegation on their leaves, (8) Near Eastern members of the Asteraceae with yellow spines, form Müllerian mimicry rings of spiny plants.

To consider the existence of Müllerian mimicry rings in aposematic organisms, two factors are needed: (1) a similar signal, and (2) an overlapping distribution in respect to the territory of predators in animals, or herbivores in plants. I will show below that for the plant taxa proposed here to form Müllerian mimicry rings, both criteria operate.

The accumulating data about the common association of plant defenses by spines with visual conspicuousness, along with the fact that many such species overlap in their habitat, raises the possibility of the broad phenomenon of existence of Müllerian mimicry rings in plants. Even from the limited number of publications proposing visual aposematism in spiny plants, the operation of vegetal Müllerian mimicry rings seems to be obvious. The phenomenon can now be traced to both the Old World (Asia, Africa and Europe) and the New World (North America). The best-studied cases include Cactaceae and the genera *Agave*, *Aloe* and *Euphorbia*,[6] African acacias with white thorns,[12,15] Near Eastern spiny plants with white variegation on their leaves,[7,11] aposematic spiny vascular plants of southeastern Ohio,[16] and many spiny Mediterranean species of the Asteraceae with yellow spines.[22]

In the four spiny taxa (Cactaceae and the genera *Agave*, *Aloe* and *Euphorbia*) that were the first to be proposed as visually aposematic[6] there is a very strong morphological similarity. In cacti, there are two types of conspicuousness of spines that are typical of many plant species: (1) colorful spines, and (2) white spots, or white or colorful stripes, associated with spines on the stems. These two types of aposematic coloration also dominate the spine system of *Agave*, *Aloe* and *Euphorbia*. The fact that many species of three of these four spiny taxa (*Agave*, *Aloe* and *Euphorbia*) are also poisonous[36-38] further indicates their potential to form Müllerian mimicry rings.

I propose that each of these groups for itself and some of these groups (e.g., Cactaceae and the genus *Agave* in North America;

*Aloe*, *Euphorbia* and acacias in east and south Africa) that have overlapping distribution and share at least some of the herbivores, form Müllerian mimicry rings.

The first Müllerian mimicry ring is of cacti and *Agave* that have an overlapping distribution over large areas in North America.[37,39] The large herbivores in North America disappeared not so long ago in evolutionary time scales and seem to have shaped the spiny defense of these plant taxa.[40]

The second Müllerian mimicry ring is of the spiny and thorny members of the African genera *Aloe*, *Euphorbia* and certain acacias with very conspicuous white thorns, which partly overlap in distribution and share various large mammalian herbivores.[12,15,36,41]

The third Müllerian mimicry ring is the outcome of the common presence of aposematic coloration in spiny vascular plants of southeastern Ohio,[16] with color patterns in thorns and spines similar to those of Cactaceae and the genera *Agave*, *Aloe* and *Euphorbia* described in Lev-Yadun.[6]

The next case of potential operation of Müllerian mimicry ring of spiny plants with overlapping territories that suffer from the same large herbivores, but on a much smaller geographical scale, has recently been proposed for several spiny species with white-variegated leaves,[7] and later for more than 20 spiny species in the flora of Israel that have white markings associated with their spines.[11]

The last case of a probable Müllerian mimicry ring was described by Ronel et al.[22] who while studying the spine system of Near Eastern spiny members of the Asteraceae, found 29 spiny species with yellow spines, and additional such species are expected to occur. Since some of these species and others with yellow spines also grow in southern Europe, it is clear that the same phenomenon is also common there.

I conclude that Müllerian mimicry rings seem to be very common in plants, and that it is probable that many other spiny plants that form Müllerian mimicry rings are waiting to be studied. Such defensive rings are probably also formed by poisonous plants that share similar colors or odors.

## References


1. Cott HB. Adaptive coloration in animals. London, GB: Methuen & Co., Ltd 1940.
2. Edmunds M. Defence in animals. A survey of anti-predator defences. Harlow, UK: Longman Group Ltd 1974.
3. Gittleman JL, Harvey PH. Why are distasteful prey not cryptic? Nature 1980; 286:149-50.
4. Savage JM, Slowinski JB. The colouration of the venomous coral snakes (family Elapidae) and their mimics (families Aniliidae and Colubridae). Biol J Linn Soc 1992; 45:235-54.
5. Ruxton GD, Sherratt TN, Speed MP. Avoiding attack. The evolutionary ecology of crypsis, warning signals and mimicry. Oxford, UK: Oxford University Press 2004.
6. Lev-Yadun S. Aposematic (warning) coloration associated with thorns in higher plants. J Theor Biol 2001; 210:385-8.
7. Lev-Yadun S. Why do some thorny plants resemble green zebras? J Theor Biol 2003; 244:483-9.
8. Lev-Yadun S. Weapon (thorn) automimicry and mimicry of aposematic colorful thorns in plants. J Theor Biol 2003; 244:183-8.
9. Lev-Yadun S. Defensive coloration in plants: a review of current ideas about anti-herbivore coloration strategies. In: Teixeira da Silva JA, ed. Floriculture, ornamental and plant biotechnology: advances and topical issues. Vol IV. London, UK: Global Science Books 2006a; 292-9.
10. Lev-Yadun S. Aposematic (warning) coloration in plants. In: Baluska F, ed. Plant-environment interactions. From sensory plant biology to active plant behavior. Berlin, Germany 2009; 167-202.
11. Lev-Yadun S. Müllerian and Batesian mimicry rings of white-variegated aposematic spiny and thorny plants: a hypothesis. Isr J Plant Sci 2009; In press.
12. Midgley JJ, Botha MA, Balfour D. Patterns of thorn length, density, type and colour in African Acacias. Afr J Range For Sci 2001; 18:59-61.
13. Lev-Yadun S, Ne'eman G. When may green plants be aposematic? Biol J Linn Soc 2004; 81:413-6.
14. Lev-Yadun S, Ne'eman G. Color changes in old aposematic thorns, spines and prickles. Isr J Plant Sci 2006; 54:327-33.
15. Midgley JJ. Why are spines of African Acacia species white? Afr J Range For Sci 2004; 21:211-2.
16. Rubino DL, McCarthy BC. Presence of aposematic (warning) coloration in vascular plants of southeastern Ohio. J Torrey Bot Soc 2004; 131:252-6.
17. Speed MP, Ruxton GD. Warning displays in spiny animals: one (more) evolutionary route to aposematism. Evolution 2005; 59:2499-508.
18. Halpern M, Raats D, Lev-Yadun S. Plant biological warfare: Thorns inject pathogenic bacteria into herbivores. Environ Microbiol 2007; 9:584-92.
19. Halpern M, Raats D, Lev-Yadun S. The potential anti-herbivory role of microorganisms on plant thorns. Plant Signal Behav 2007; 2:503-4.
20. Lev-Yadun S, Gould KS. Role of anthocyanins in plant defense. In: Gould KS, Davies KM, Winefield C, eds. Life's colorful solutions: the biosynthesis, functions and applications of anthocyanins. Berlin, Germany: Springer-Verlag 2008; 21-48.
21. Lev-Yadun S, Halpern M. External and internal spines in plants insert pathogenic microorganisms into herbivore's tissues for defense. In: Van Dijk T, ed. Microbial ecology research trends. New York, NY: Nova Scientific Publishers, Inc 2008; 155-68.
22. Ronel M, Khateeb S, Lev-Yadun S. Protective spiny modules in thistles of the Asteraceae in Israel. J Torrey Bot Soc 2009; 136:46-56.
23. Inbar M, Lev-Yadun S. Conspicuous and aposematic spines in the animal kingdom. Naturwissenschaften 2005; 92:170-2.
24. Wiens D. Mimicry in plants. Evol Biol 1978; 11:365-403.
25. Shapiro AM. Egg-mimics of Streptanthus (Cruciferae) deter oviposition by *Pieris sisymbrii* (Lepidoptera: Pieridae). Oecologia 1981; 48:142-3.
26. Williamson GB. Plant mimicry: evolutionary constraints. Biol J Linn Soc 1982; 18:49-58.
27. Ehleringer JR, Ullmann I, Lange OL, Farquhar GD, Cowan IR, Schulze E-D, Ziegler H. Mistletoes: a hypothesis concerning morphological and chemical avoidance of herbivory. Oecologia 1986; 70:234-7.
28. Niemelä P, Tuomi J. Does the leaf morphology of some plants mimic caterpillar damage? Oikos 1987; 50:256-7.
29. Launchbaugh KL, Provenza FD. Can plants practice mimicry to avoid grazing by mammalian herbivores? Oikos 1993; 66:501-4.
30. Augner M, Bernays EA. Plant defence signals and Batesian mimicry. Evol Ecol 1998; 12:667-79.
31. Lev-Yadun S, Inbar M. Defensive ant, aphid and caterpillar mimicry in plants. Biol J Linn Soc 2002; 77:393-8.
32. Lev-Yadun S. Defensive functions of white coloration in coastal and dune plants. Isr J Plant Sci 2006b; 54:317-25.
33. Lev-Yadun S, Ne'eman G, Shanas U. A sheep in wolf's clothing: Do carrion and dung odours of flowers not only attract pollinators but also deter herbivores? BioEssays 2009; 31:84-8.
34. Soltau U, Dötterl S, Liede-Schumann S. Leaf variegation in *Caladium steudneriifolium* (Araceae): a case of mimicry? Evol Ecol 2009; In press.
35. Lev-Yadun S, Gould KS. What do red and yellow autumn leaves signal? Bot Rev 2007; 73:279-89.
36. Reynolds GW. The Aloes of South Africa. Cape Town, South Africa: A.A. Balkema 1969.
37. Gentry HS. Agaves of continental North America. Tucson, AZ: University of Arizona Press 1982.
38. Nobel PS. Remarkable agaves and cacti. New York, NY: Oxford University Press 1994.
39. Benson L. The cacti of the United States and Canada. Stanford, CA: Stanford University Press 1982.
40. Janzen DH. Chihuahuan Desert nopaleras: Defaunated big mammal vegetation. Annu Rev Ecol Syst 1986; 17:595-636.
41. Sajeva M, Costanzo M. Succulents the illustrated dictionary. Portland, OR: Timber Press 1994.