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When may green plants be aposematic?

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During the long, dry summers, the deserts of the Middle East are almost devoid of green plants. In the summer, most annuals, geophytes and hemicryptophytes either are dormant in the soil or have already been eaten by the grazing flocks. Many shrubs are summer deciduous or enter summer dormancy with minimal green canopy. However, there are several common plants that, contrary to the general phenology, are conspicuously green during summer, when all the surroundings are yellow. In such conditions, green is conspicuous and contrasts with the background, as do yellow, red and black in 'greener' ecosystems. The summer-green plants are also characterized by being poisonous or thorny as protection against herbivory. During winter and spring, when there are plenty of other green, more palatable annual plants, herbivory pressure is much lower and they need less protection. We propose that during summer in the dry desert, when most other plants are dry or indistinctive, a vivid green colour can be aposematic.

ADDITIONAL KEYWORDS: aposematic coloration – desert – grazing – herbivory – olfactory aposematism – poisonous plants – thorns.

INTRODUCTION

Aposematic coloration, a well-known phenomenon in animals (Cott, 1940; Edmunds, 1974; Gittleman & Harvey, 1980; Harvey & Paxton, 1981; Mallet & Joron, 1999), has been shown recently to be common in thorny plants as well (Lev-Yadun, 2001, 2003a,b). Strong and contrasting colours (red, yellow, black, brown or various colour patterns including white stripes) usually characterize aposematic unpalatable or poisonous species (Cott, 1940; Edmunds, 1974; Gittleman & Harvey, 1980; Lev-Yadun, 2001). The probable evolutionary rationale behind these strong aposematic colours of organisms is that they stand out from the background, deterring the target organisms (predators or herbivores), which can easily see them and remember the visual signal (Gittleman & Harvey, 1980; Harvey & Paxton, 1981; Mallet & Joron, 1999). Green plants dominate most productive terrestrial ecosystems (Hairston, Smith & Slobodkin, 1960). Therefore, green can neither be conspicuous nor aposematic under such conditions. Knight & Siegfried (1983) raised the question of whether green fruits signal unpalatability, and concluded that in the forest green does not provide enough contrast to be aposematic.

Water availability is the main limiting factor for plant growth in deserts. In the hot deserts of the Middle East, the rainy season is restricted to several months in winter and spring. Therefore, desert plants have developed various adaptive strategies to survive during the long, hot and dry summer (Evenari, Shanan & Tadmor, 1982; Archibold, 1995). Annual plants survive the dry season as dormant seeds in the soil; geophytes and hemicryptophytes pass the summer as dormant underground corms, bulbs or roots. Shrubs and dwarf-shrubs drastically reduce their leaf area and canopy size in summer by shedding leaves and branches, or by replacing large winter leaves with smaller summer ones to lower their water loss. Their summer leaves are usually covered by dense white trichomes that reflect the radiation from the sun, thus reducing transpiration (Orshan, 1963, 1986; Evenari *et al.*, 1982). Other plants have succulent leaves or stems with a very thick waxy cuticle layer that considerably reduces transpiration during daytime when their stomata are closed. Many succulents have

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adopted the CAM photosynthetic pathway, opening their stomata at night rather than during day (Winter & Smith, 1996). Winter and spring are the main growing seasons for the vast majority of the annual and perennial Middle Eastern desert plants. Therefore, at the landscape scale, the dominant landscape colour during winter and spring is green. At the beginning of the summer, annuals complete their lifecycle and dry up, as do the aboveground parts of geophytes and hemicryptophytes. Shrubs and dwarf-shrubs that retain live canopies during summer lose most or all of their green parts. As a result, the landscape turns yellow. Surprisingly, there are some conspicuously green plant species in the summer that contradict this general phenological pattern.

Here, we present several cases of common poisonous or thorny plants that keep their vital green colour during the summer in the heavily grazed, nearly plantless, yellow landscape in the Negev Desert in Israel. We propose that the conspicuously green colour is aposematic.

METHODS

As a part of a broader study on the ecology of vegetative coloration in plants (see Lev-Yadun, 2001, 2003a,b; Lev-Yadun & Inbar, 2002; Lev-Yadun *et al*., 2002), grazed areas in the west, north, east and central parts of the Negev Desert, Israel, were inspected repeatedly, in all seasons, during the years 1990–2002. Special attention was given to regions densely populated by Bedouins who own large flocks of sheep and goats (cattle, donkeys and camels are much less abundant). We monitored conspicuously summer-green plants that were avoided by the numerous browsing flocks. Additional data on grazing avoidance were compiled from Danin (1977), and Shmida & Darom (1986), and on poisonous plants from Waisel, Cohen & Binyamini (1977). Taxonomy follows Feinbrun-Dothan, Danin & Plitmann (1991).

RESULTS AND DISCUSSION

Grazing by flocks of animals owned by Bedouin almost completely harvests the low plant biomass of the desert. In the summer, in large heavily grazed areas, the remaining plants become extremely sparse. However, even under such drastic grazing pressure, there are several common plant species that are conspicuously green but are not eaten by the herds. It is clear that the flocks see the green plants because they eat all other dry but palatable plants around them, but leave them untouched. All these plants are poisonous or thorny.

The poisonous group includes the green desert shrub *Ephedra aphylla* Forssk. (= *E. alte* C.A. Meyer) (Ephedraceae), which contains ephedrin (Caveney *et al*., 2001). The shrub *Pergularia tomentosa* L. (= *Daemia tomentosa* (L.) Pomel) (Asclepiaceae) and the small tree *Calotropis procera* (Aiton) Aiton fil. (Apple of Sodom), growing in hot but humid habitats, are poisonous like most members of the family, which are rich with saponins and alkaloids (Waisel *et al*., 1977). The aposematic grasshopper *Poekilocerus bufonius* sequestrates the poisons of *Calotropis procera* for self-protection (Euw *et al*., 1967). Three very common species, *Anabasis setifera* Moq., *A. syriaca* Iljin and *A. articulata* (Forssk.) Moq. (Chenopodiaceae), are also alkaloid-rich summer-green shrubs that are not eaten by the flocks (Zohary, 1980; Feinbrun-Dothan *et al*., 1991). The common geophyte *Asphodelus ramosus* L. (= *A. aestivus* Brot. = *A. microcarpus* Salzm. et Viv.) of the Liliaceae has poisonous green leaves that are not grazed in the winter, but are eaten when dry and brown in the summer (Seligman *et al*., 1959; Shmida & Darom, 1986). The perennial herb *Peganum harmala* L. of the Zygophyllaceae is very poisonous and not eaten by the flocks. Therefore, it is very common near Bedouin camps where the flocks eat its competitors (Danin, 1977). Like *P. harmala*, the shrub *Thymelaea hirsuta* (L.) Endl. of the Thymelaeaceae is also poisonous, is not eaten by the flocks, and is abundant near Bedouin camps (Shmida & Darom, 1986). The summer annuals *Chrozophora tinctoria* (L.) A. Juss. and *C. obliqua* (Vahl) Sprengel (Euphorbiaceae) are also avoided by the flocks. Another member of the Euphorbiaceae, the introduced tall shrub *Ricinus communis* L. (castor oil plant), also remains green but is not grazed. Of the Solanaceae, the introduced shrub *Nicotiana glauca* Graham, the shrub *Withania somnifera* (L.) Dunal, and the summer annuals *Datura innoxia* Miller, *D. stramonium* L. and *Solanum nigrum* L. are all alkaloid-rich poisonous plants (Waisel *et al*., 1977) with a strong deterrent smell, especially when wounded, and they are not eaten by the flocks.

The thorny plant group includes the shrubs *Alhagi graecorum* Boiss. (= *A. maurorum* Medicus) (Papilionaceae) and *Zilla spinosa* (L.) Prantl (Brassicaceae), which have green stems and branches even in the summer, after their summer leaf shed. Both species are extremely thorny. The shrubs *Capparis aegyptia* Lam. and *C. sinaica* Veillard (= *C. cartilaginea* Decaisne) (Capparaceae), found in rocky habitats in the desert, are both very spiny, as is the shrub *Asparagus stipularis* Forssk. (Liliaceae), which retains green stems during the summer.

Thus, the small number of common plants that are green in the dry summer in the Negev Desert (Israel), when most other plants are either totally dry (annuals, geophytes and hemicryptophytes) or are summer deciduous, have good protection against herbivory either by being poisonous or thorny. Although sheep and goats consume all other plant species around them, they avoid these summer-green plants. The impact of millennia of selective grazing by the flocks owned by nomad and seminomad people has resulted in the dominance of these species in the summer vegetation of the Negev. It is tempting to suggest that these summer-green plants have shifted their season of activity as their protective devices have developed. Thus, this is an analogue for an evolutionary colour change in conventional aposematic organisms. Interestingly, and in support of our hypothesis, plants that are evergreen in predominantly deciduous forests, plants leafing or flowering especially early in spring in the temperate region, or spring ephemerals in Great Britain, i.e. plants that are green when their neighbours are not, have a high incidence of toxicity (Grubb, 1992). We propose that in various arid and other types of ecosystems, when most plants are dry or leafless, green colour is conspicuous and contrasts with the yellow desert or leafless background and can act as an aposematic colour. However, it is clear that green cannot be aposematic in environments where it does not contrast with the background. Thus, green fruits posted against green canopy cannot serve as an aposematic colour as proposed by Knight & Siegfried (1983). Moreover, most of the proposed aposematic summer-green plants are green also during winter, when their colour cannot be aposematic because at that time they are surrounded by many other green plants that are winter annuals. Secondary compounds are usually found at lower levels in deciduous leaves with a short life span and in ephemeral plants than in evergreen leaves of perennial plants with a long life span (Price, 1997). As a result, during winter, the summer-green aposematic plants are protected from herbivory by their more palatable neighbours, which will be eaten first (Milchunas & Noy-Meir, 2002). The levels of secondary metabolites in these plants are subject to seasonal changes, being lower during winter and higher in summer (Price, 1997). Consequently, we hypothesize that also in desert plants the concentration of the secondary metabolites increases at the beginning of the summer when the background turns from green to yellow and the plants' green colour becomes aposematic.

The possibility of green colour acting as an aposematic signal is not different in principle from that of red, yellow or black. The colours by themselves do not signal any specific message, but rather draw attention. Red flowers or fruits usually are a positive signal for pollinators and frugivores to approach the plant (Faegri & Pijl, 1979; Pijl, 1982). Red spines, however, signal aposematism (Lev-Yadun, 2001). There are red, yellow and black attractive fruits or yellow or red attractive flowers along with red, yellow and black aposematic colours of animals or thorny plants. If these colours can serve for both attraction and aposematism, there should be no theoretical reason to discount green as an aposematic colour also.

Some of the poisonous summer-green plants (i.e. *Calotropis*, *Datura*, *Nicotiana*, *Ricinus*, *Thymelaea*) also have specific strong deterrent odours, especially when damaged. This fact supports the hypothesis of olfactory aposematism in poisonous plants (i.e. Eisner & Grant, 1981; Launchbaugh & Provenza, 1993; Provenza, Kimball & Villalba, 2000) and the proposal that multimodal signals are more effective than simpler ones (Lindström, Rowe & Guilford, 2001). It is possible that olfactory aposematism in poisonous plants is more common than previously realized. In an almost plant-less arid environment a strong deterrent odour combined with a conspicuous colour may be an easy-to-remember aposematic combination. The higher concentration of volatile secondary metabolites during summer increases both the repellent odour and the levels of poisonous substances (Price, 1997) in these plants when they are at their greenest. In this way, the green plant colour becomes aposematic.

We conclude that green plants may be aposematic during the almost plant-less summer in deserts and that some of these poisonous plant species also use olfactory aposematism to communicate with herbivores for their mutual protection. Their ability to avoid even causal tasting by grazers is critical for their survival in the highly grazed Negev Desert or similar ecosystems.

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