Further evidence that in African acacia, white is a warning colour to herbivores: the white pseudo-galls of *Vachellia seyal*

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Pseudo-galls of three East African acacia (*Vachellia*) species were compared to determine the correlates of gall colour and their potential defensive functions. Although all three species produce white thorns, the pseudo-galls of *V. gerrardii* and *V. drepanolobium* are dark coloured. In contrast, pseudo-galls of *V. seyal* var. *fistula* are white. Associated with this, they are thin-walled and poorly used by aggressive mutualistic ants. We suggest that this weak functionality is compensated for by the highly visible white colour. This aposematism may also involve mimicry as only the *fistula* variety of *V. seyal* has galls and only this variety co-occurs with other *Vachellia* species that have functional galls. *Vachellia seyal seyal* does not have pseudo-galls and this variety does not occur with other *Vachellia* species that have pseudo-galls.

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Visual aposematism, the defence brought about by warning colouration, is a newly emerging and controversial field in plant biology (Lev-Yadun 2001, 2009). The best examples are of colourful thorns, spines and prickles, but also warning colouration of poisonous organs including leaves, stems, flowers and fruits (Lev-Yadun 2009). The thorns of most African acacia, now *Vachellia* and *Senegalalia* (see Kyalangalilwa et al. 2013) species, are white, whereas hooks (recurved spines) are cryptic (green or brown that match background leaves and stems) (Midgley et al. 2001).

The thorns of many other species are cryptic. Midgley (2004) suggested that the white colouration of these thorns warns large herbivores where the thorns are. Aside from primates, most eutherian mammals are dichromatic (Jacobs 2009). White is an important signalling colour for the achromatic contrast aspect of vision for dichromatic animals, such as the white tail signalling used by many herbivores to warn approaching carnivores (Bildstein 1983). This is in contrast to the red, yellow and orange aposematic colours often used as chromatic aposematic signals used for polychromatic animals. It is beneficial for herbivores to avoid contacting and/or consuming thorns as they are not nutritious and wounding by thorns, especially to the eyes, would be painful and dangerous, especially because some thorns harbour pathogenic microorganisms (Halpern et al. 2007).

The benefit of white thorns to plants is that being conspicuous means they will not be consumed or blunted (sharp tips bitten-off) and thus these thorns would still serve to modify herbivore feeding rates of leaves. Also, white thorns may act as aposematic signals to reduce the incidence of herbivores approaching some branches or individual plants. A further benefit is that white thorns are hollow and thus relatively few resources are used to construct them compared with woody, but more cryptic thorns (Midgley 2004). Besides thorns, in some African acacia species thorns swell up enormously to produce pseudo-galls, which may be inhabited by aggressive mutualistic ants. In this paper we focus on the white colour of the pseudo-galls in *Vachellia* (*Acacia*) *seyal* var. *fistula* (Supplementary Figure S1). Pseudo-galls have not previously been considered as a potentially visually aposematic organ. Recently, the colour and shape of parasite-induced true galls have been considered to be aposematic (Inbar et al. 2010; Gerchman et al. 2013).

This scenario is different to that concerning pseudo-galls because, in the former case, gall aposematism is a potentially protective signal by the parasitic insect against insectivores, not for or by the plant against herbivores.

The best-studied African pseudo-gall (henceforth gall) is the whistle-thorn acacia, *Vachellia drepanolobium*. It has an assemblage of aggressive ant mutualists (Madden and Young 1992; Young et al. 1997) that make use of the galls as well as food glands on the plant. Despite its thorns being white, its galls are darkly coloured (brown to purple-brown)

At our study site with *V. drepanolobium*, co-occurring is *V. gerrardii* which has dark galls and *V. seyal* var. *fistula* which has white galls. Ant-inhabited galls in acacia range from an occasional swollen thorn, such as some *V. gerrardii* individuals at our site but also elsewhere including *V. eriophora*, *V. horrida* and *V. bussei* (Ross 1979), to true pseudo-galls such as *V. drepanolobium* and *V. seyal*.
var. fistula, but elsewhere also including V. zanzibarica, V. bullockii, V. malaecocephala, and V. pseudofistula. All of these gall species have dark galls (Ross 1979).

Following the above logic regarding white thorn colour, we predict that the galls of Vachellia will differ inversely in apparentness and functionality; specifically, that white galls will also be (1) large, but (2) will have thinner walls and be less frequently used by any ants (lower frequency of access holes, and lower occupancy by ants), especially aggressive ants.

This field study was carried out during 18–24 September 2013 in Segera Ranch, which is located in Laikipia County in central Kenya. Of the different acacia species found in the ranch, three species produce galls: V. drepanolobium, V. gerrardii and V. seyal var. fistula.

We pruned off one healthy branch (i.e. no signs of herbivory) of 1 cm diameter between 1 and 2 m above the ground for each of 20 individuals of each acacia species, and in the laboratory measured the diameter of the largest gall per branch with a pair of callipers. We cut through the gall and measured the maximum thickness of the gall’s wall, using a leaf thickness meter. In the field, one healthy gall per individual tree was inspected for the presence of an access hole (n = 25–42) and whether ants occupied the gall. We noted the presence of only the most common and aggressive gall-ant species (Crematogaster mimosae, C. nigriceps, C. sjostedtii and Tetraponera penzigii; based on Young et al. 1997) in the galls.

All V. drepanolobium individuals had galls and access holes and of these 55% had the very aggressive ants Crematogaster mimosae or Crematogaster nigriceps present and a further 40% had Tetraponera penzigii in the galls (Table 1). Although all V. seyal fistula individuals had galls, only 32% of galls had an access hole and only 20% of galls had ants in them. Tetraponera penzigii was found in these five galls (Table 1). Vachellia seyal fistula thus has statistically lower observed occurrence of ants in galls than V. drepanolobium (chi-square, p < 0.001). Of 42 V. gerrardii individuals, 25 plants had galls and, of these, 76% had holes in the galls. Of these 19 plants, nine harboured Tetraponera penzigii (Table 1).

Despite being similarly sized to V. drepanolobium galls, the galls of V. seyal fistula were less attractive to ants; they had by far the lowest percentage of ant-utilised galls (20% versus 95%) and total absence of the two most aggressive ant species (C. nigriceps and C. mimosae). Young et al. (1997) previously noted C. sjostedtii on a low frequency of V. seyal fistula galls, but did not investigate galls or gall-ants in V. gerrardii.

The relative lack of aggressive ants in V. seyal fistula galls does not seem to be due to an absence of leaf glands to provide nutrition to ants, as the variety has adaxial leaf glands (Ross 1979). Possibly, aggressive ants avoid the thin galls of V. seyal fistula because they receive less protection within these galls. Vachellia seyal fistula has thinner galls than V. drepanolobium (Mann–Whitney, p < 0.03). Protection maybe from marauding ants or from vertebrate predators such as patas monkeys (Erythrocebus patas). The latter derive up to 30% of their daily caloric needs from ant larvae within V. drepanolobium galls (Isbell and Young 2007). Also, competing ant species fight for access to galls via entrance holes. Thus, some ant species defend themselves from attack by making small access holes, which attacking species then try to enlarge (Young et al. 1997). Thin gall walls would allow greater access to the interior of galls and/or to the larvae within galls and therefore be less attractive to ants.

Both V. drepanolobium and V. seyal fistula are preferred food plants of large mammalian herbivores (Young et al. 1997) and thus will benefit from being defended. However, the galls of V. seyal are likely to be much less efficient in providing ant defence against these herbivores. What then is the function of these galls? Interestingly, only the fistula variety of V. seyal has galls. Vachellia seyal var. seyal does not have galls (Ross 1979). Only V. seyal fistula occurs on the black cotton soils that V. drepanolobium also occurs on (Coe and Beentje 1991). Coe and Beentje (1991) hypothesised that in these specific edaphic habitats, the annual wet-season inundation prevents ants foraging on the ground for a period of the year. Galls thus facilitate an arboreal existence. That V. drepanolobium and V. seyal fistula co-occur raises the potential that V. seyal fistula galls are conspicuous mimics of the former. If so, white galls may function similarly to white thorns; they may act as flags to influence which individuals or branches are approached by herbivores and at a finer scale they may influence feeding patterns within a branch as herbivores avoid biting or disturbing these conspicuous galls. The alternative hypothesis for only V. seyal fistula having ant galls, is habitat-driven convergence. However, this is less likely than mimicry given that V. seyal fistula galls are only weakly attractive to aggressive ants. Vachellia drepanolobium galls are not conspicuously coloured so that herbivores mistakenly disturb the aggressive ants that they house.

Midgley (2004) and Lev-Yadun (2009) noted that coloured plant organs have several likely costs and therefore they should have benefits to compensate for this. Similarly to thorns, galls are white and will thus produce

Table 1: Gall characteristics of three Vachellia species

| Characteristic                  | V. seyal var. fistula | V. gerrardii | V. drepanolobium |
|--------------------------------|-----------------------|--------------|------------------|
| Percentage plants with galls (n) | 100 (25)              | 60 (42)      | 100 (25)         |
| Percentage galls with holes (n)  | 32 (25)               | 76 (25)      | 100 (25)         |
| Percentage galls with aggressive ants | 20                   | 36            | 95               |
| Gall diameter (cm; SD)          | 3.01 (0.8)            | 2.12 (0.4)   | 2.93 (0.6)       |
| Gall wall thickness (mm; SD)    | 0.79 (0.2)            | 1.87 (0.4)   | 1.35 (0.2)       |
no or less photosynthate and they will also incur the direct white pigment costs. Secondly, white galls will be highly conspicuous to herbivores. We suggest that conspicuousness is traded-off against functionality. We predict that *V. seyal fistula* individuals will suffer lower herbivory rates with conditioned herbivores than they will with herbivores that have not experienced aggressive ants associated with galls. Also, we suggest that experimental *V. seyal fistula* plants without galls (removed or white colour hidden) will suffer higher herbivory levels than control plants.

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