Defensive ant, aphid and caterpillar mimicry in plants?

SIMCHA LEV-YADUN* and MOSHE INBAR

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

Received 22 January 2002; accepted for publication 21 August 2002

Here we describe three apparently novel types of visual insect mimicry in plants. In the first type, plants of *Xanthium trumarium* L. have dark spots and flecks that resemble ants (Formicidae) in size and shape in the epidermis of stems, branches and petioles, and plants of *Arisarum vulgare* Targ.-Tozz. have them on petioles and inflorescence stems. In the second type, the dark anthers of *Paspalum paspaloides* (Michaux) Scribner (= *P. distichum*) are the size, shape and colour of aphids (Homoptera; Aphidoidea) and they sway in the wind like swivelling aphids. Similarly, the stems of *Alcea setosa* (Boiss.) Alef. are covered with dark flecks that look like aphids. Finally, immature pods of three wild annual legumes (*Lathyrus ochrus* (L.) DC.; *Pisum fulvum* Sm.; *Vicia peregrina* L.) have conspicuous reddish spots, arranged along the pods, that appears to mimic lepidopteran caterpillars. In one of the species (*V. peregrina*) two different mimicking morphs were found. We propose that these morphological traits may serve as herbivore repellent cues and are part of the defence system of the plants. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 77, 393–398.

ADDITIONAL KEYWORDS: Aposematic – herbivory – insect – repellent.

INTRODUCTION

It is widely accepted that some invertebrate and vertebrate animals visually masquerade as parts of plants and thus gain protection from predators (Cott, 1940; Wickler, 1968; Edmunds, 1974). Classic examples listed in Cott (1940) include: several species of fish and crabs that resemble algae; geckos and moths that look like lichens; many insects, amphibians and reptiles that masquerade as leaves; tree bark mimicked by spiders, moths, beetles, amphibians, lizards and birds; stick-insects (Phasmida) that resemble branches; and flower masquerade by thomisid spiders and bugs.

Much less attention has been paid to mimicry of animals by plants. The best-known case are orchids of the genus *Ophrys* that mimic female bees and are thus pollinated by male bees that are attracted to them (Wiens, 1978; Dafni, 1984). The dark spots on the umbels of wild carrot (and several other species of Apiaceae) consist of dark central flowers that may mimic insects and thus attract potential insect pollinators (Eisikowitch, 1980). Similarly, black spots on the ray florets of *Gorteria diffusa* (Asteraceae) resemble aggregation of resting bee flies (Johnson & Midgley, 1997).

Only rarely has animal mimicry been proposed in plants as a means of avoiding herbivore damage. Egg mimicry in plants has been proposed to reduce egg laying in *Heliconius* butterflies (Benson, Brown & Gilbert, 1975; Gilbert, 1980; Shapiro, 1981a; Williams & Gilbert, 1981). In addition, an example of possible indirect animal mimicry in plants is the supposed resemblance of caterpillars feeding damage on the leaf lobes of some Moraceae (Niemelä & Tuomi, 1987).

If visually searching herbivores avoid previously colonized host plants, or if such leaves attract predators and parasitoids that prey on herbivores of these plants, than such mimicry would be beneficial to the plant.

Plants employ many physical, chemical, temporal and mutualistic defence mechanisms against herbivory (Crawley, 1983; Howe & Westley, 1988). The role of mimicry in general and of animal mimicry in particular in anti-herbivory has received very little attention. Related issues of plant–animal communication via vegetative parts, such as aposematic coloration, which are commonplace for zoologists, are only now being recognized as important for plant biology (Lev-Yadun, 2001; Lev-Yadun et al., 2002).
Here we describe three novel types of a plant part visually resembling an animal, which we interpret as mimicry of an insect by the plant: dark spots and flecks that mimic ants, dark anthers that mimic aphids, and immature legume pods ornamented with colourful spots that mimic caterpillars.

OBSERVATIONS

ANT MIMICRY

The stems, branches and some of the petioles of *Xanthium trumarium* (Asteraceae) are characterized by scattered conspicuous dark-coloured dots and flecks usually 2–10 mm in size (Fig. 1). Dots predominate in some individual plants, flacks in others. Similarly, the petioles and inflorescence stems of *Arisarum vulgare* Targ.-Tozz. (Araceae) are covered by many dark flecks. Thus, to the human eye the shoots of these two species appear to be covered by a swarm of ants. Ant swarms are typically made of many moving dark flecks, each varying in size from several mm to over 1 cm. The swaying of leaves, stems or branches in the wind in combination with the dark spots and flecks, some of which are arranged in lines, may give the illusion that the ‘ants’ move.

APHID MIMICRY

The anthers of *Paspalum paspaloides* (Poaceae), a wind pollinated plant, are about 2–3 mm long, dark-coloured, and dangle from the green inflorescences, gently moving with the wind (Fig. 2). The anthers thus appear to be covered by dark aphid colonies (Homoptera: Aphidoidea, e.g. *Aphis, Toxoptera* and *Macrosiphum*). Similarly, the stems of *Alcea setosa* (Bois.) Alef. (Malvaceae) are covered with dark flecks that look like aphids (Fig. 3). Many species of aphids tend to aggregate on young stems and leaves of their host plants (Fig. 4) (Dixon, 1998), and two common polyphagous species *Sipha maydis* Passerini and *Rhopalosiphum maidis* (Fitch), both 2–3 mm long, are found on many species of the Poaceae.

CATERPILLAR MIMICRY

The immature pods of three wild legume species: *Pisum fulvum* (Figs 5,6), *Lathyrus ochrus* (Fig. 7) and *Vicia peregrina* (Fabaceae) (Figs 8,9) have conspicuous spots of several shades of red. *Vicia peregrina* has two distinct morphs. Red spots characterize the first (Fig. 8), resembling those of *L. ochrus* and *P. fulvum*. Red circles with green centres, the pods characterize the second morph (Fig. 9). All these pods mimic the general shape, size and colour of lepidopteran caterpillars ornamented with spiracles or other spots on their sides such as a pieride moth (Pieridae) (Fig. 10).

DISCUSSION

Both authors were easily confused when trying to evaluate whether dark flecks and spots were ants or aphids from distances larger than 1 m. The resemblance of the dark spots and flecks to ants and the dark anthers to aphids was found to be close enough to cause both authors confusion on first view of spotted plants as if they were covered with ants or aphids. Similarly, aphid-covered stems were considered on first view to be spotted. Likewise, the legume pods described appeared to be caterpillars. We propose that these colour patterns comprise three novel types of defensive insect mimicry in plants. What could be the benefit of these types of mimicry? We suggest that they may signal unpalatability to more than one group of animals in two ways: first, insect mimicry may reduce attacks by insect herbivores that refrain from colonizing or feeding on infested plants (because of competition and/or induced plant defences); and second, where the insect mimicked is aposematic, this could deter larger herbivores from eating the plants (Figs 1,5,6–9).

REDUCING COLONIZATION OF INSECTS

Among other chemical and visual (shape, size and colour) cues, insects can visually detect and assess previous infestation during the process of host plant selection (Vinse, 1976; Rothschild & Schoonhoven, 1977; Rausher, 1979; Shapiro, 1981b; Bernays & Chapman, 1994). It has been proposed that egg mimicry by plants may reduce egg laying by butterflies (Benson et al., 1975; Gilbert, 1980; Shapiro, 1981a; Williams & Gilbert, 1981). The same effect should apply to butterflies if they refrain from laying eggs on plants that already appear to be infested, such as the legume pods that mimic caterpillars. Interestingly, Rothschild (1974) has suggested that the stipules of some *Passiflora* are modified to look like horned caterpillars, thus reducing female oviposition. Several studies have shown that early infestation by aphids and other homopterans has a negative impact on host plant preferences and larval performance of other insect herbivores. Finch & Jones (1989) reported that large colonies of the cabbage aphid *Brevicoryne brassicae* (L.) and the peach aphid *Myzus persicae* (Sulz.) deter ovipositioning by the root fly *Delia radicum* (L.). This seems to be a common phenomenon in aphid–herbivore associations (studies by A. F. J. Dixon and colleagues, cited in Finch & Jones (1989)). Inbar Doostdar & Mayer (1999) demonstrated that homopterans (whiteflies) not only alter adult cabbage looper (*Trichoplusia ni* (Hübner) Lepidoptera: Noc-tuidae) host selection, but also actually reduce the feeding efficiency of their offspring. Aphids respond to
DEFENSIVE INSECT MIMICRY IN PLANTS

Figures 1–4. Fig. 1. A stem of *Xantium trumarium* covered with conspicuous dark-coloured dots and flecks that look as if they were covered by an ant swarm. Fig. 2. The dark-coloured anthers of *Paspalum paspaloides* dangle from the green inflorescences and look as if dark aphids covered them. Fig. 3. A stem of *Alcea setosa* covered with dark flecks that look like aphids. Fig. 4. Dark aphids feeding on a young stem.
crowding by enhanced dispersal (Dixon, 1998) and it is thus also probable that they may avoid previously infested or infestation-mimicked hosts.

**Deterrence of feeding by large herbivores**

Caterpillars employ a large array of defences that reduce predation, such as camouflage, mimicry of their enemies’ predators, physical shelters and chemical defences (Bowers, 1993). Unpalatable caterpillars with stinging and irritating hairs, functional osmeteria or body-fluid toxins often advertised their presence by aposematic coloration and aggregation (Cott, 1940; Bowers, 1993). The usual warning colours are red, yellow, black and white with stripes along the body and/or arranged in spots, especially around the abdominal spiracles. Aposematism in caterpillars should reduce predation for several reasons, including an innate tendency of vertebrates to avoid warning colours and faster avoidance learning of bright as opposed to cryptic colours (Coppinger, 1970; Gibson, 1980; Lindström, Rowe & Guilford, 2001). Therefore we suggest that by mimicking aposematic caterpillars with red ‘spiracle spots’ wild legumes may reduce immature pod predation. It has been shown that ungulates may actively select leaves in the field by shape and colour and avoid spotted ones (e.g. Cahn & Harper, 1976) but we have failed to find data on the response of vertebrate herbivores to aposematic (or cryptic) caterpillars. However, personal information from colleagues indicates that in some systems caterpillars may deter herbivore feeding (A. Perevolotsky and R. Harmsen pers. comm.).

The potential benefit from ant-attendance mimicry is obvious. Ants bite and sting and are aggressive and most insectivorous animals and herbivores will avoid them. Thus, ants have become models for a variety of arthropods that have evolved to mimic them (Edmunds, 1974). Plants may benefit if ants protect them from insect and mammalian herbivory (Madden & Young, 1992; Julivet, 1998). In a field experiment, removal of ants and aphids resulted in an increase of 57% in species richness, and their abundance increased by 80% (Wimp & Whitham, 2001). Moreover, ant and aphid removal also resulted in a 76% increase in the abundance of other herbivores on narrow-leaf cottonwoods (Wimp & Whitham, 2001). Many plant species invest considerable resources in attracting their enemies’ predators, physical shelters and chemical defences (Bowers, 1993). Unpalatable caterpillars with stinging and irritating hairs, functional osmeteria or body-fluid toxins often advertised their presence by aposematic coloration and aggregation (Cott, 1940; Bowers, 1993). The usual warning colours are red, yellow, black and white with stripes along the body and/or arranged in spots, especially around the abdominal spiracles. Aposematism in caterpillars should reduce predation for several reasons, including an innate tendency of vertebrates to avoid warning colours and faster avoidance learning of bright as opposed to cryptic colours (Coppinger, 1970; Gibson, 1980; Lindström, Rowe & Guilford, 2001). Therefore we suggest that by mimicking aposematic caterpillars with red ‘spiracle spots’ wild legumes may reduce immature pod predation. It has been shown that ungulates may actively select leaves in the field by shape and colour and avoid spotted ones (e.g. Cahn & Harper, 1976) but we have failed to find data on the response of vertebrate herbivores to aposematic (or cryptic) caterpillars. However, personal information from colleagues indicates that in some systems caterpillars may deter herbivore feeding (A. Perevolotsky and R. Harmsen pers. comm.).

The potential benefit from ant-attendance mimicry is obvious. Ants bite and sting and are aggressive and most insectivorous animals and herbivores will avoid them. Thus, ants have become models for a variety of arthropods that have evolved to mimic them (Edmunds, 1974). Plants may benefit if ants protect them from insect and mammalian herbivory (Madden & Young, 1992; Julivet, 1998). In a field experiment, removal of ants and aphids resulted in an increase of 57% in species richness, and their abundance increased by 80% (Wimp & Whitham, 2001). Moreover, ant and aphid removal also resulted in a 76% increase in the abundance of other herbivores on narrow-leaf cottonwoods (Wimp & Whitham, 2001). Many plant species invest considerable resources in attracting...
ants, providing them with shelter, food bodies and extrafloral nectaries (Huxley & Cutler, 1991). Other plants may tolerate aphid infestation to gain anti-herbivore protection from aphid-attending ants (Bristow, 1991; Dixon, 1998). We argue that the aggressive and efficient anti-herbivore activities of ants makes it highly beneficial for plants, such as X. trumarium and Arisarum vulgare, to mimic ant attendance in order to deter herbivores without paying the cost of feeding or housing them.

Some flowers mimic animals (Dafni, 1984), indicating that animals can both act as models for mimicry in plants and select for such phenotypes. Animal mimicry as a defence mechanism against herbivores has largely been overlooked. Although not tested empirically, a game theory based model has predicted that mimicry of plant defence signals might be common (Augner & Bernays, 1998). Furthermore, if herbivores tend to avoid signalling plants, selection allows the invasion by even poor and imperfect mimics (Augner & Bernays, 1998; Edmunds, 2000). Recently, it has been demonstrated that many thorny plants advertise their mechanical defence to herbivores by colourful thorns or associated coloration (Lev-Yadun, 2001). Our findings further indicate that the role of plant coloration/shape in anti-herbivore defence deserves more attention and that the adaptive significance of the described apparent mimicry merits further examination.

ACKNOWLEDGEMENTS

We thank M. Edmunds, T. G. Whitham and an anonymous referee for their helpful comments and insight.

REFERENCES


Cott HB. 1940. Adaptive coloration in animals. London: Methuen Ltd.


