MIMICRY IN CARNIVOROUS PITCHER PLANTS — FACT OR LEGEND?

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Patterns of shape and colour together with tactile and olfactory stimuli form guiding signals for insects in pitcher plants. Many parallels may be drawn between the mechanisms by which traps allure prey and those used by flowers to attract insects for pollination. It is often argued that the traps of carnivorous pitcher plants serve as mimics simulating properties of nectar-producing flowers (visual as well as olfactory), and that these properties attract flower-pollinators which are thus deceived, trapped and digested. In this way, according to Williamson (1982), the pitcher plants share the feature of capturing insects who have innate floral preference, or provision experience with flower models, but little or no experience with the trap.

This concept is widely accepted though having no experimental basis.

When reviewing the attraction mechanisms in carnivorous plants for our new textbook on these plants (Juniper, Robins and Joel 1988) I first found myself caught under the mimetic concept, but then gradually developed a growing suspicion towards it which led me to a thorough examination of the problem. As a result I have developed a new interpretation of the available information. Accordingly, a comprehensive review of the subject was recently published in the Botanical Journal of the Linnean Society (Joel (1988) and a whole chapter is devoted to this problem in our book. In the following I present the main points of the new concept.

What does mimicry mean?

Mimicry involves an organism (the mimic) simulating signals of another living organism (the model) which are perceived by a third living organism (the operator) as signals of interest, such that the mimic gains in fitness as a result of the operator identifying it as an example of the model (Vane-Wright 1980). When a rare, non-rewarding species mimics the more abundant 'provider', this deceptive mimetic system is classified as "Batesian Mimicry" (Pasteur 1982). The known deceptive mimics in the plant kingdom are mainly flowers, which interact with insects for pollination (Dafni 1984).

The supply of a compensating reward like nectar by the more common model is essential in order to subsidize the system. By definition, reward is never provided by the mimic.

Frequent deception will either lead to selective pressures against the mimic, or enable the operator to learn to avoid it. Hence, a successful mimic will build either scattered, small populations, or large populations which are active for a short while.

Do pitcher plants behave like mimics?

The traps of the carnivorous pitcher plants of the Sarraceniaceae, Nepenthaceae and Cephalotaceae do not fit important characteristics of a typical mimetic system.

Unfortunately, no study is available which compares insect pollinators and insect victms in the same habitat. Gibson (1983), who studied the North American pitcher plants, is of the opinion that certain species specialized in capturing insect taxa known to visit regularly non-carnivorous flowers blooming in the same habitat. Two points weaken the possibility of deceit mimicry in these cases. Firstly, there is often a temporal separation between the flowering period of associated flora and the trapping period of the pitchers. Secondly, pitcher plants are generally most active in capturing insects during their growth phase immediately after fire or drought when other flowering plants are far behind in forming their own community.

The populations of pitcher plants are often extremely large and dense. In certain species of *Sarracenia* they may attain phenomenal densities under regimes of repeated disturbances from fires, drought and heavy grazing. In these cases we may assume that certain insects, hatching in this same area, do not leave the boundaries of the pitcher plant population and are therefore attracted only to pitcher plants, not to neighboring plant communities.

All pitcher plants are perennial, their traps being active for long seasons. Once a pitcher plant is established, it will provide a fairly regular supply of new pitchers over a number of years in a restricted area.

Extensive and dense stand of *S. leucophylla*. Photo by B. Hanrahan.

All these characteristics of the plant community of pitcher plants are not compatible with a deceptive status, and contradict a minetic strategy.

Perhaps the most significant feature of carnivorous pitcher plants which contradicts a mimetic status is their production of nectar, which is a real energetic reward. The traps of all pitcher plants secrete nectar, which is composed of a watery solution of sugar and is believed to contain amino acids as well. It is secreted mainly at the peristome and the hood. Nectar is very often also secreted on other parts of the pitcher, along the veins on the soutside of *Sarracenia* pitchers, along the 'fishtail' of *Darlingtonia* and along the 'wings' on the front of *Nepenthes* and *Cephalotus* pitchers.

The nectar secreted by pitcher traps is usually interpreted as an attractant, tempting insects to reach the trapping site and remain there until they stumble and fall into the digestive cavity where they are consequently digested. In flowers, nectar is regarded as an energetic and nutritional reward to pollinators. Likewise, extrafloral nectaries are supposed to support insects which confer services, like defense, to the plant. While visual and olfactory patterns of attraction are utilized both by traps and by deceptive mimetic flowers, nectar is not provided by floral mimics (Dafni 1984).

In many cases a large proportion of the insect visitors can be seen to consume nectar and leave the traps unharmed. This is particularly obvious in pitchers which are visited by ants. Traffic in two directions is often observed on these pitchers, which in indicative of the rewarding nature of their nectar. Surprisingly, the mean number of insects captured daily in a single pitcher is small in spite of the relatively high rates of visits per pitcher. For example, out of hundreds of ants visiting a *Cephalotus* pitcher every day only a few are consumed by the plant.

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Many insects manage to visit several pitchers during their stay in the pitcher habitat, and might also visit the same pitcher several times without being trapped.

The rate of insect capture, the structure of the plant community and, above all, the provision of nectar, rule out the possibility that pitcher plants adopted a mimetic strategy.

Instead, could mutualism apply to this system?

Mutualism is defined as an interaction between species that is beneficial to both (Boucher *et al.* 1982). The difference between mutualism and deceptive mimicry is in the bidirectional benefit of the former. Benefit is gained in the latter only by one side in the interspecific interaction. Perhaps the best example of mutualism in the plant kingdom is the interrelations between flowers and insect pollinators.

The data discussed above have lead me to suggest that pitcher plants resemble insect-pollinated flowers in that they serve as "nectar suppliers" in their habitats. In return, small portions of the insect communities, which benefit from the nectar provided by the pitcher plants, are 'sacrificed' and serve as prey.

This system can be mutually beneficial: The pitcher plants feed visiting insects with nectar, by which they support the insect community in their poor habitat where flowers and other sources of nectar are often uncommon or absent. The insects, in return, pay the plants with a small portion of their community which is trapped and digested. The plants, which commonly live in nutrient deficient habitats, benefit from the digested prey which provides an alternative source for certain absent soil nutrients.

The pitcher plants can provide sufficient amounts of nectar, because they grow in moist and sunny habitats where water supply and photosynthetic energy are not limited and thus the production of carbohydrate is relatively cheap.

Insects will return to the same pitchers or to similar pitchers if they have gained some profit during their first visit. They will rapidly learn that the visual and olfactory characteristics, typical of the pitchers in their vicinity, lead them to a reliable source of nectar. Those few insects which pay for the nectar with their lives cannot transfer their 'knowledge' of the possible danger, simply because they die. Selection against visits will not develop because the proportion of 'casualties' is limited.

Conclusion

Pitcher plants do not strictly mimic flowers; they resemble flowers. Both flowers and pitchers use insects for some sort of benefit, i.e. pollination and nutrition, respectively, and both pay the insects with energetic nectar. In evolutionary terms flowers and pitcher traps seem therefore to have formed convergent strategies.

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