FLOWER/INSECT INTERRELATIONS - A CASE OF UNUSUAL PREDATION

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Received 16 September 1987, 23 March 1988

ABSTRACT: Evolutionarily early flower-like structures such as Cycadeoidales, were undoubtedly subjected to heavy predation by browsing insects. These ancestoral flowers, as those other plant organs, developed a typical defense system that enabled them to contend with damage caused by their predators.

From the moment when predators began to serve (even accidentally) as pollen vectors and thereby raised the survival rate of plants by contributing pollination, prey-predator balance entered into conflict. Normally, preyed-upon species "do their best" to remove themselves from their predators. However, in the case of flowering plants a total success in this respect would mean lowering the chances of pollination and a subsequent total failure of the plant to continue to exist. The evolutionary response was the development of two parallel trends: a defensive system of sensitive organs against predators on the one hand and the production of alternative bait, such as food bodies or nectar, on the other. It was necessary also for the flower to develop a very efficient advertising program, sending signals to predators by directing them to a desirable place within the flower. The predation within the flower then resulted in the process of pollination. Such an interrelationship can show an unusual dependence of prey upon its predator.

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INTRODUCTION

Although the origin of angiosperms is obscure and has been the subject of debate for a long time (Baker and Hurd 1968, Kevan 1984), the general agreement is that the ancestors of flowers were on plants of the order Cycadeoidales (Bennettitales) (Foster and Gifford 1974, Takhtajan 1969). This group of plants is specially characterized by a bisporangiated strobilus, consisting of a conical receptacle which bears ovules and microsporophylls containing numerous microsporangia (Foster and Gifford 1974).

These cycad-like plants, which flourished during the Mesooic Era, were exposed at that time to insects, which had been abundant since the late carboniferous Era (Leppik 1960, 1963).

In spite of the scanty fossil evidence up to now for insect pollination of early angiosperms, there is good reason to suggest that the first zoophilic pollinations probably occurred accidentally during predation on the rich proteins or amino acids in "flower" spores by mandibulated Coleoptera foraging opportunistically among flowers as well as among other vegetative targets (Baker and Hurd 1968; Crepet 1979; Janzen 1971; Leppik 1960, 1967, 1975; Price 1984; Gottsberger 1977).

Early conflicts of interest in pollination

Our starting point is that pollinating insects might be considered, at least in their early contacts with flowers, as herbivores (Crepet 1979) or parasites (Leppik 1975). As the Coleoptera and other important pollen- and ovule-feeding insects in the Triassic became more common, they became also more elaborate in their chewing abilities. However, they could also be more important as pollinators and this phenomenon probably resulted in a growing conflict of interests, as the damage caused by the chewing insects called for

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Evolutionary Theory 8: 151-154 (May, 1988)
The editors thank H.W. Kerster and another referee for help in evaluating this paper.

the appearance of some sort of defense mechanism by the plants against the herbivores. Such a change may take place either chemically, morphologically, anatomically or by alterations in the behavior of the plant, which ultimately will react by indulging in an "arms race" (Dawkins and Krebs 1979). Such behavior might end in the extinction of one or both opponents, or by certain compromises such as occurred in many other parts of the plant, like thorns, poisonous leaves or stems, etc. However, in the flower/insect interaction, such a situation is different and more complicated: if the predator could overcome the defensive barrier of the flower, the flower would either cease the production of exposed spores or, if the plant should be completely successful in self-defense and deter the predator from its target, it will lose the service of the insect as a vector for its male spores. This conflict was settled by various compromises based on partial defense of certain targets: one solution was achieved by the trend to ovule defense by means of integuments, inferior ovaries (Grant 1950), and zygomorphic or tubular flowers with few stamens and much more concealed pollen grains. Food bodies, of various origins, which exist in certain flowers can be easily explained as an alternative offering which will deter the hungry, chewing insects from the more sensitive organs to those which are less vulnerable (Baker and Hurd 1968). However, any use of mandibles for grazing damaged the flowers, not only by physical destruction but also by exposing it to micro-organism contamination.

Shifting from grinding towards sipping

The main breakthrough by flowers was probably achieved when nectaries appeared in the flower. In this way the predator was exploited but in a way less injurious to the flower, since the collection of food in the form of a solution does not cause the damage to the flower (see also Kevan 1984). This turning point of shifting the food target from "grinding" towards "sipping" probably directed the evolution toward longer-tubed flowers (Leppik 1957, 1972), lengthening of petals and sepals and creation of various methods of nectar containers. The nectar location became very important in relation to the location of the pollen grains and the direction of the entry of the insects into the flowers. All these trends of evolution were probably followed by the evolution of insects with more elongated mouth parts (Goldman 1933).

The reduction of chewable, parts of the "flower", rich in amino acids, could cause a shortage in amino acids for the insects and was probably followed by selection of nectar richer in amino acids. This can be an explanation for the assumption that the nectar in higher plants is richer in amino acids than in lower plants (Baker and Baker 1973).

Flower-insect interrelationship

The outcome of such selection resulted in a bizarre situation for the plant/insect relationship. The prey built up a system that offered a portion of itself to a predator. However, this target was situated in such a very distinct position as to compel the predator to arrive at it by only a certain path, which meant that there was a closed circuit between pollen and stigma, i.e., a topocentric pollination (Galil 1973, Kevan et al. 1983). Flowers not only offer parts of themselves to predators, but they also develop an elaborate system that emits signals which attract the predator or even inform the predator of its exact nectar/pollen situation (Gori 1983, Eisikowitch and Lazar 1987).

Scanning the zoology literature shows that communication between prey and predator has existed (at least, according to several zoologists). Warning calls, for example, usually considered as a signal by which the preyed-upon individual warns others of its species of the presence of a predator (an apparently altruistic behavior described by Maynard-Smith 1965) was recently explained also alternatively as a communication system between prey and predator (Smythe 1970, Zahavi 1977). Such an explanation can also be adopted in the case of the flowers and pollinators, i.e., during evolution, the preyed-upon plants, by turning the food target into less easily damaged parts, establish a communication system with their predators and directed them away from being phytophagous predators towards being anthophyles, and thence into their obedient servants.

This paper is more historical reconstruction viewed from prey-predator possible interaction rather than an argument of an ecological optimality.

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ACKNOWLEDGEMENTS

Thanks are due to Mrs. Ruth Direktor who edited and typed the manuscript.

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