Floral mimicry: a fascinating yet poorly understood phenomenon
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Flowers of different species that resemble each other are not necessarily mimics. For mimicry to be occurring, the similarity must be adaptive. Unfortunately, no case of floral mimicry has ever been fully verified and it is important that we move beyond these perceived similarities to testing whether they are truly adaptive. Here we explain the differences between Batesian and Müllerian floral mimicry, illustrate what should be done to test mimicry hypotheses, and discuss how interspecific pollen transfer influences the evolution of mimicry.

The concepts of Batesian and Müllerian mimicry have been developed by zoologists and are commonly associated with protective mimicry in animal systems. However, these concepts also apply to plant systems because the same evolutionary processes that govern them (negative and positive frequency-dependent selection) occur when an animal is being warned away (protective mimicry) or invited in (floral mimicry). In animal Batesian mimicry, selection favors resemblance of a palatable mimic to an unpalatable model. Similarly, in Batesian floral mimicry, selection favors resemblance of a rewarding model to a non-rewarding mimic to a rewarding model. In animal Müllerian mimicry, selection favors resemblance of non-mimic species to other non-mimics. In botanical Müllerian mimicry, selection favors resemblance of different non-mimic species to the same rewarding model species.

For floral mimicry to be established as occurring between two or more similar species, they must:
- Have strongly overlapping distributions, and must have done so long enough for co-evolution to have occurred.
- Require pollinators for seed set.
- Overlap substantially in flowering phenology.
- Share the same pollinator species and the same individual pollinators must move freely between the species.
- The similarity must be important for fitness.

The majority of floral mimicry studies establish the first four points, but either neglect or incompletely address the last point – the critical question of whether the similarity is actually adaptive. Before we suggest the tests necessary to assess the fitness consequences of similarity, we would first like to further describe the basic kinds of floral mimicry, because the type of mimicry influences the kinds of tests performed. There are two basic types of floral mimicry, Batesian and Müllerian, which are governed by different selection regimes (Fig. 1). In Batesian floral mimicry, the mimic produces no nectar reward, whereas the model does (Fig. 2). Hence the mimic’s chances of visitation should be increased through its similarity to a nectar-producing model. Further, because the Batesian mimics do not have nectar, the more frequent they are in the population, the lower their pollination success becomes because pollinators can learn to avoid flowers that look a certain way, and indeed, both mimic and model might be avoided. Thus, new Batesian mimic phenotypes that mimic a different model will enjoy a pollination advantage and this type of negative-frequency-dependent selection should select for increased diversity of model–mimic pairs (Fig. 1).

In Müllerian floral mimicry, two or more rewarding model species gain a collective advantage as a result of convergence on a ‘common advertising display’... The similarity of Müllerian mimics increases the ‘perceived’ density of rewarding flowers and, thus, might increase the probability of pollinator visitation (Fig. 3). When pollinator visitation is positively density-dependent, greater similarity among flower species implies higher pollination success. Thus, Müllerian mimics are undergoing positive frequency-dependent selection (Fig. 1), and are all converging on a similar phenotype. In spite of selective pressure towards similarity, variation in Müllerian mimics probably exists because pollinators...
vary across the range of a species, and might change from one part of the season to another.

Several differences between the two basic types of floral mimicry should now be clear. In Batesian mimicry, only the model is rewarding, whereas in Müllerian mimicry, all the species present pollinators with rewards. In Batesian mimicry, the model does not gain from the interaction, whereas in Müllerian mimicry, all the species gain an advantage as a result of their similarity. In Batesian mimicry, there is an obvious model on which the mimic is based, whereas in Müllerian mimicry, it is always a more common phenotype. First, one could create artificial repetitions that lack the features associated with the mimicry, and test whether these individuals have lower fitness than those with greater similarity to the model. Second, one could determine whether the putative mimics have the same or even higher fitness when they co-occur in a patch as they do in separate, same-density patches of the individual species. In other words, do insects treat all the members of a Müllerian mimic ring as if they were the same, choosing when to forage based on the number or density of similar shaped, colored or scented flowers, rather than on the specific species composition of the patch? Some preference by pollinators might occur, but, on average, patch density, not patch composition should determine the fitness of flowers of similar appearance.

Interspecific pollen transfer and evolution of mimicry

There is a limit to how similar co-flowering, sympatric species can be to each other, because individuals need to be able to mate with the proper species. If two flower species look too much alike, vision might transfer their pollen to the wrong species, a phenomenon called improper pollen transfer. Improper pollen transfer, which is a form of competition, will tend to select for differences among species. A plant’s success will be enhanced if a pollinator transfers its pollen directly to another of the same species. Thus, improper pollen transfer could reduce selection for mimicry unless it is ameliorated in some way.

Because there are examples of floral mimicry, we can look at these species to learn how improper pollen transfer can be decreased. Orchids, the group with the most mimetic species (up to a third of the known orchids, or ~10 000 species according to some estimates), package their pollen in saddlebag-like structures called pollinia. It is suggested that pollinia are less likely to be improperly transferred than pollen because pollinia tend to be like keys, fitting only into flowers with the proper shape. However, in spite of pollinia, hybridization is thought to be common in orchids. Another trait that might be important for co-flowering species is flower longevity. As long as the likelihood of hybridization is low, and the presence of foreign pollen on a stigma is not itself harmful, mimetic flowers that can wait until the proper pollen arrives will have an advantage. The evolution of the Costus alleli-C. lavii mimicry system (Fig. 3) might have been favored by a combination of long flower longevity and strong barriers against hybridization. The pseudoflowers produced by flower-mimic fungi are also long-lived, producing nectar for

There are two alternative methods for testing floral Müllerian mimicry hypotheses when there is little or no phenotypic variation in the putative mimics. First, one could create artificial phenotypes that lack the features associated with the mimicry, and test whether these individuals have lower fitness than those with greater similarity to the model. Second, one could determine whether the putative mimics have the same or even higher fitness when they co-occur in a patch as they do in separate, same-density patches of the individual species. In other words, do insects treat all the members of a Müllerian mimic ring as if they were the same, choosing when to forage based on the number or density of similar shaped, colored or scented flowers, rather than on the specific species composition of the patch? Some preference by pollinators might occur, but, on average, patch density, not patch composition should determine the fitness of flowers of similar appearance.

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experiments have long-lived flowers 30,31. However, it is also possible that clumped distributions might increase the likelihood of proper pollen transfer because they attract more visitors as a result of their combined density, and the fact that each of the individual species grows in clusters might also increase the likelihood of proper pollen transfer 32-34. However, it is also possible that clumped distributions might increase the ability of the pollinators to distinguish mimics from models and choose one over the other 32. Experiments are needed to determine the relative importance of clustering in influencing pollinator behavior and to determine whether improper pollen transfer is reduced.

Competition favors character divergence and has thus sometimes been thought to be antithetical to the evolution of mimicry 14,15. However, competition for visitors can lead directly to selection favoring similarity, if one species is favored over another, and if morphs that have greater similarity to the preferred species receive more visits and have higher pollination success and fitness (positive frequency-dependent selection, Fig. 1). Of course, selection can operate independently of phytotypic similarity for pollinator attraction and improper pollen transfer. For example, if visitors are density-dependent, and pollinators use visual cues for deciding where to forage, then selection will favor the convergence of flowers towards similar coloration, shape and size. Simultaneously, there might also be selection to decrease the degree of improper pollen transfer, and, thus, differences in the shape and length of anthers would be favored if they contacted pollinators’ bodies in different places 14, or if pollen is scraped off on-nature reproductive flower parts 15. The outcome of simultaneous selection for visual similarity and differential pollen placement might yield something like the red tubular-flowered guild that attract hummingbirds in the southwestern USA, in which the different species place the pollen on hummingbirds in different places. Indeed, this guild has been suggested to be a Müllerian mimicry ring 15, although not all of the species have similar pollinator visitation preferences.
the critical tests of Müllerian mimicry suggested here have been performed. Another incompletely tested hypothesis suggests that 
flowers (and fungi) might sometimes attract 
visitors with visual cues, which allows the 
evolution of visual similarity, but simulta-
neously produce different fragrances that 
might influence insect constancy at close 
range\textsuperscript{35,36}.

Competition is commonly cited for causing 
differences in flowering phenologies\textsuperscript{34,35} (but see Ref. 39 for an alternative view). Although species that 
flower at different times will partition the available pollinators among 
them, species pairs that are similar to one 
another might gain an advantage early in their 
flowering season when they overlap because there will be no "lag" period as pollinators 
adjut to a new morphology\textsuperscript{45}. This mechanism 
might operate in the red-flowered, beetle-
pollinated guild in Israel\textsuperscript{41} and in co-occurring 
yellow-flowered composite\textsuperscript{30} (Fig. 3).

Areas for future research
Although Müllerian mimicry has been sug-
gested for several species of similar appear-
ance that share pollinators, no one has performed 
the crucial tests to determine whether the simi-
larity is adaptive (Fig. 3). If none of the puta-
tive cases of Müllerian mimicry is a true 
example, then this suggests that improper 
pollen transfer is a severe constraint on the 
evolution of floral mimicry. However, we 
suspect that experimental evidence will soon 
establish Müllerian mimicry as a fact in the 
plant world.
The two major kinds of mimicry are governed by different types of selection – negative or positive frequency-dependent selection (Fig. 1). These two kinds of selection allow us to make predictions about the degree of morphological variation that one should expect to see in different kinds of mimicry systems. In Batesian floral mimicry, where no reward is offered by the mimic, a large amount of phenotypic variation is to be expected because the more common a mimetic phenotype is, the more it will be actively avoided by pollinators[9,15]. For Müllerian floral mimicry, on the other hand, Little variation in the mimetic phenotype is to be expected because the commoner the phenotype is, the higher its fitness is, and this kind of positive frequency-dependent selection ultimately leads to fixation of the most common phenotype (Fig. 1). Although these statements about polymorphism under the two kinds of selection are generally expected to be true, research on mimicry in butterflies has found the patterns of variation to be the opposite of expectations (reviewed in Ref. 19). We currently have too little information on the degree of phenotypic variation in flower mimics to make any general statements about patterns, although it appears that orchids might support the predicted pattern for Batesian mimics. Considerable morphological variation has been reported in orchid species that have been suggested to be Batesian mimics (reviewed in Ref. 9). Again, this variation is expected to be adaptive, because variation in the mimic will reduce the ability of pollinators to learn to avoid non-rewarding flowers[16].

Botanists lag far behind their zoological counterparts in terms of understanding the genetics of mimicry. We have no solid understanding of any traits involved in floral mimicry systems, and thus cannot test models suggesting that the evolution of mimicry is a two-step process[20]. Furthermore, there are no tests of basic phylogenetic hypotheses concerning mimicry. For example, does deceptive pollination always evolve from reward pollination systems[21]? Another obvious phylogenetic question, as yet untested in floral mimicry, is do species in Müllerian rings show evidence of co-evolution? Finally, the importance of the “signal perceiver” or “operator” should not be forgotten in this process involving the perception of pollinators and the signaling capabilities of plants and some fungi. There is no reason to expect that selection for mimicry will be the same from one species to the next, or from one geographic area to another. Experimental approaches replicated throughout the flowering season and across geographic ranges are required to study floral mimicry, yet they have almost never been applied. Thus our understanding of floral mimicry remains in its infancy.

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