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Helping in food-deceptive orchids?

A possible new mechanism maintaining polymorphism of floral signals

Laurent Dormont,[1,*] Roxane Delle-Vedove,[1] Jean-Marie Bessière,[2] Martine Hossaert-Mc Key[1] and Bertrand Schatz[1]

[1]Centre d'Ecologie Fonctionnelle et Evolutive; UMR 5175 CNRS; Montpellier, France; [2]Ecole Nationale Supérieure de Chimie de Montpellier; Laboratoire de Chimie Appliquée; Montpellier, France

Why different color morphs have evolved in flowering plants, and how they are maintained in populations, have long intrigued ecologists. The impact of variation in floral color and odor (the two are frequently associated) on reproductive success remains poorly understood. In European rewardless orchids, many species occasionally show rare white-flowered individuals within populations of the common-colored morph. In a recent study, we found that in *Orchis mascula* the presence of rare white-flowered morphs significantly increased the reproductive success (from 6% to 27%) of purple-flowered plants, while success of the white morph remained low. This surprising result appears due solely to floral color polymorphism, which in this species is not associated with odor polymorphism. We hypothesize that color variation plays the key role in pollinator attraction, and that white-flowered individuals may be regarded to function as "sensory traps". We also propose that the maintenance of white-flowered mutants in *O. mascula* may result through kin selection, in which they act as helpers increasing the reproductive success of related purple individuals.

Key words: floral polymorphism, color, odor, reproductive success, *Orchis mascula*, rewardless orchid, helper

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*Correspondence to: Laurent Dormont; Email: laurent.dormont@cefe.cnrs.fr

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Many flowering plants are characterized by considerable variation in floral traits at individual or population levels.[1,2] Pollinator-mediated selection is often proposed to explain the maintenance of floral polymorphism: for example, variation in plant signals such as floral color or floral odor has been reported to be associated with various pollinator preferences.[3,4] In fact, very few studies have examined the simultaneous effects of both color and odor polymorphism on pollinator attraction and plant reproductive success.[5]

Food-deceptive orchids have flowers that contain no nectar but mimic floral signals of rewarding plants to attract pollinators. In these plants, high variation in floral signals is thought to be associated with adaptations to maximise pollinator attraction: deceptive flowers must delay the avoidance learning of pollinators.[6,7] One spectacular aspect of intraspecific color variation in orchids is the occurrence of rare white inflorescences within populations of colored inflorescences.[1,8] Whether the presence of rare white-flowered morphs is the product of only recurring spontaneous mutations or is the consequence of pollinator-mediated selection remains an intriguing question. We found that the frequency of white-flowered variants (1%) in some orchid species, e.g., in *Orchis mascula*, a food-deceptive orchid distributed throughout Europe, was about 10 times higher than that predicted where recurring spontaneous mutations affect floral pigmentation genes and observed in other plant families.[9,10]

In a recent study,[11] we showed that floral scent did not differ between white- and purple-flowered morphs of *O. mascula*. We hypothesize that odor signals do not help pollinators to distinguish between color morphs, and that color variation alone probably plays the key role. The reproductive success of the purple morph, estimated by the average fruit set, was low (6%) in populations with only purple inflorescences. Surprisingly,

when populations of purple-flowered plants included a few white-flowered individuals, the fruit set of the purple morph increased significantly (from 6% to 27%), while that of the white morph remained low (6%). We obtained the same fourfold increase in fruit set by using white ping-pong balls as visual lures in pure populations of the purple morph.

Naive flying pollinators probably avoid homogeneous patches of *O. mascula* purple morph after unrewarding visits to purple flowers, whereas the white/purple color contrast exhibited by mixed patches remains attractive to naïve or recently deceived insects. Such color contrast may even be regarded to function as a "sensory trap", in the sense defined by Christy:[12] "sensory traps are signal mimics that exploit the adaptive neural responses of signal receivers to elicit out-of-context behaviors". In our system, white morphs did not experience a direct selective advantage from the signal emitted, as has been found in other sensory trap models.[13,14] It could be hypothesized that *O. mascula* functions as a sensory trap that benefits groups of individuals.

How the maintenance of rare white morphs can be explained in evolutionary time remains difficult to answer. Among a few hypotheses we have proposed,[11] kin selection might provide a possible explanation for our results. In *O. mascula*, the presence of white-flowered variants might benefit neighboring, related purple-flowered morphs. Such "helping" of individuals by relatives has not been demonstrated in plants. However, many plant populations show spatial genetic structure, with related individuals being aggregated, as has already been shown in the genus Orchis.[15] The effect of so-called helpers on reproductive success has been described for a diversity of cooperative breeding systems in vertebrates.[16,17] In plants, kin selection has been invoked to explain why some plants compete less severely with relatives than with nonrelatives,[18,19] but whether helpers may occur in plant populations has not yet been explored. Helping, in a restricted definition, is probably not fully consistent with the situation found in *O. mascula*, in that helping in animal communities is supposed to be a temporary, transient behavior (helpers further become breeders), and also implies inhibiting one's own reproduction.[16] Nonetheless, we here suggest that rare white-flowered morphs in *O. mascula* may be considered helpers that allow increased reproductive success of neighboring purple individuals. We are currently examining this hypothesis, based on kin selection, which would represent a new mechanism that may explain the maintenance of color polymorphism in plants. How floral signals function in the reproductive strategies of non-rewarding orchids results from complex and diverse processes;[7] our study provides a new and original example of such diversity.

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