

## Effects of hybridization and selection on floral isolation

(mechanical isolation/hummingbird pollination/hawkmoth pollination/introgression/*Ipomopsis*/*Aquilegia*/*Diplacus*)

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**ABSTRACT** This paper examines the case of natural hybridization between two angiosperm species (A and B) which are mechanically and ethologically isolated (or florally isolated). What is the effect of hybridization on the pollination system, and conversely, what is the effect of the pollinators on the outcome of the hybridization? The original floral isolation is based on an interspecific differentiation in floral characters, the floral mechanisms of the parental species being specialized for pollination by different types of pollinators with different body forms and behavioral traits. F<sub>1</sub> hybrids of A × B have intermediate floral characters and serve as bridges for interspecific cross-pollination. The problem next shifts to the changes in floral characters and mode of pollination that are likely to occur in later generations in the hybrid population. The pollinators of species A and species B exert selective pressures on the hybrid population. If the normal pollinator of A is more abundant, active, and effective in the hybrid population than the pollinator of B, selection is expected to favor a reversion toward the floral characters and pollination system of A. The opposite condition, in which the pollinator of B is predominant, leads to the reciprocal result, reversion toward B. If the two types of pollinators are more or less the same in number of flower visits and pollination effectiveness, their combined selective pressure should produce later-generation derivatives with intermediate floral characters suited for both pollinators. Three western North American plant groups containing florally isolated species that hybridize (*Ipomopsis*, *Diplacus*, and *Aquilegia*) are examined in relation to these predictions. The evidence in the three groups is generally in agreement with the hypothesis.

Mechanical and ethological isolation often occur together in angiosperms and are referred to collectively as floral isolation. The floral isolation is frequently incomplete. A pair of florally isolated species may remain reproductively isolated in one area of sympatric contact but hybridize in another area. This pattern has been reported in a number of genera: *Aquilegia* (Ranunculaceae) (1–4), *Epimedium* (Berberidaceae) (5), *Ipomopsis* (Polemoniaceae) (4, 6–8), *Penstemon* (Scrophulariaceae) (9), *Diplacus* (Scrophulariaceae) (10), *Rhinanthus* (Scrophulariaceae) (11), *Salvia* (Labiatae) (12), and *Platanthera* (Orchidaceae) (13).

We understand why the floral isolation breaks down locally. Floral isolation operates in conjunction with ecological isolation (4). Both modes of isolation are sensitive to man-made or natural disturbances of the original habitat differences between the related sympatric species. We have descriptive and analytical studies of the hybrids between florally isolated species in various plant groups. The initial hybridization is known to be followed by introgression in the species groups in six of the genera listed above: *Aquilegia* (1), *Ipomopsis* (6, 7), *Diplacus* (10, 14), *Rhinanthus* (11), *Salvia* (12), and *Platanthera* (13).

However, there has been no systematic examination of the effects of hybridization between florally isolated species on the pollination systems. What modes of pollination develop

in the later-generation progeny of the hybrids? What factors determine the results?

This paper deals with the latter questions. A hypothesis is proposed in a special and general form. The special hypothesis is stated in terms of florally isolated species pairs in which one species is primarily hummingbird-pollinated and the other hawkmoth-pollinated. This hypothesis is examined in the light of evidence from three species groups containing ornithophilous species, sphingophilous species, and interspecific hybrid progeny. The special hypothesis can be extended to other paired combinations of pollination systems.

### THE POSTULATED PROCESS

The starting point of the process is a pair of outcrossing plant species that are sympatric, more or less interfertile, and separated by ecological, mechanical, and associated ethological isolation. The two species are adapted for visitation and pollination by hummingbirds and hawkmoths, respectively. We will assume that the ornithophilous flowers and sphingophilous flowers are those characteristic of the western North American flora, since the evidence to be presented later is drawn from plant groups in this area.

The mechanical and associated ethological isolation between the ornithophilous and sphingophilous species depends on a marked divergence in floral characters. The nectar-containing floral tubes of the ornithophilous and sphingophilous flowers differ in length, width, and accessibility. Nectar production in the two classes of flowers occurs at different times of day and night. Corolla color varies from red to white or other light shades, and the flowers may be fragrant or odorless. The pollen deposition mechanism differs (4). The structural differences in the flowers that inhibit access of hummingbirds to sphingophilous flowers, or vice versa, and reduce interspecific cross-pollination determine the mechanical isolation. This plays a primary role. When the birds and moths learn that they cannot obtain nectar satisfactorily by legitimate probes on the “wrong” species of flower, they resort to nectar-robbing or seek other flower species which do furnish readily accessible nectar. Ethological isolation then operates as a side effect and reinforcement of mechanical isolation (4, 15).

The external isolation is incomplete and is breached by local hybridization. Hybridization represents a reversal in the evolution of divergence in floral characters and a new trend toward convergence. F<sub>1</sub> hybrids generally have intermediate characters. Such intermediates can be expected to serve as bridges between the ornithophilous and sphingophilous parental types. The mechanical and ethological isolation is expected to be significantly reduced in populations containing F<sub>1</sub> hybrids. A hybrid swarm is likely to develop in later generations if an open or disturbed habitat exists. Mechanical and ethological isolation continues to be reduced in the hybrid swarm.

What happens in subsequent generations? The secular ecological and demographic factors that promote backcrossing and introgression are well known and well documented.

Introgression is a general phenomenon that occurs whether the parental species are differentiated in floral characters and pollination system or not. Here we are concerned with the more specific case in which the parental species have different types of pollinators.

Hummingbirds and hawkmoths are present in the local area and are part of the environment of the hybrid population. Their flower visits exert selective pressures on the hybrid progeny. Pollinating visits by hummingbirds bring about selection for ornithophilous floral characters, and pollinating visits by hawkmoths exert selection for sphingophilous characters.

The result in later generations should depend on the relative frequency of effective pollinating visits carried out by the hummingbirds and by the hawkmoths. Three main courses of selection are considered. (i) If hummingbirds are more abundant, active, and effective as pollinators in the hybrid population, the product of selection should be skewed toward ornithophilous characters. (ii) If the reverse is true and hawkmoths are the most active and effective pollinators, the progeny of the hybrids should revert toward the characters of the sphingophilous parent. (iii) If the number of pollinating visits and pollination effectiveness of the birds and moths is about the same, the combined selective pressures should produce facultative hummingbird-and-hawkmoth flowers with intermediate characters in later generations.

Selection courses *i* and *ii* can be regarded as a special form of introgression in which the controlling selective factor is the pollinating agent rather than secular ecological conditions. In these two cases, as in ordinary introgression, the derived products will approach the character combination of the recurrent parental type as a result of selection, but they will probably not completely attain the recurrent parental character state because of the persistence of some foreign genetic material. In course *iii* we have the reduction of previous specializations and the stabilization of an intermediate condition.

## MATERIALS AND METHODS

The three species groups that furnish evidence relevant to the postulated process outlined above are the *Ipomopsis aggregata* group (Polemoniaceae), *Diplacus longiflorus* group (Scrophulariaceae), and *Aquilegia formosa*–*Aquilegia caerulea* group (Ranunculaceae). *D. longiflorus* and its relatives are sometimes treated as members of the genus *Mimulus*. The three species groups have been studied from the standpoints of systematics, ecology, pollination, fertility relationships, and hybrid analysis by a series of botanists, including myself.

The groups occur in mountainous regions of western North America. Each group consists of outcrossing diploid perennial plants with ornithophilous taxa and sphingophilous taxa. The ornithophilous and sphingophilous species are broadly sympatric in *Ipomopsis* and *Aquilegia* and marginally sympatric in *Diplacus*. The species remain reproductively isolated in some areas of sympatric contact but hybridize in other areas. Internal sterility barriers are known to be weak in each group (7, 14, 16–18). The burden of reproductive isolation thus falls on external mechanisms, particularly ecological, mechanical, ethological, and seasonal isolation. Hybridization, as just noted, overcomes these external isolating mechanisms in some zones of contact.

The ornithophilous taxa of the *I. aggregata* and *A. formosa*–*A. caerulea* groups are known to be pollinated by *Selasphorus rufus*, *Selasphorus platycercus*, *Stellula calliope*, and unidentified hummingbirds; the sphingophilous taxa, by *Hyles lineata* and other hawkmoths. The scattered records are summarized and documented in a previous paper (4). Parallel records are available for the *D. longiflorus* group. The ornithophilous taxa of *Diplacus* are visited and pollinated

by *Calypte costae*, *Calypte anna*, *Selasphorus sasin*, and unidentified hummingbirds (10, 19, 20), and a sphingophilous taxon is pollinated by *H. lineata* (10).

The evidence for ecological and floral isolation in the *I. aggregata* and *A. formosa*–*A. caerulea* groups has been summarized in a previous paper (4). The parallel story for the *D. longiflorus* group is presented by Beeks (10). Hybrid analyses have been carried out in the species groups in *Ipomopsis* (6, 7, 21), *Diplacus* (10, 14), and *Aquilegia* (1).

We are concerned in this paper mainly with the following taxa in the three groups.

- 1a. Ornithophilous *Ipomopsis*; red trumpet-shaped corollas.
  - I. aggregata formosissima*; Pacific slope and southwest.
  - I. aggregata aggregata*; Rocky Mountain region.
  - I. aggregata collina*; eastern slope of southern Rocky Mountains and adjacent high plains.
- 1b. Sphingophilous *Ipomopsis*; white salverform corollas with long tubes.
  - I. tenuituba*; subalpine zone from California and Oregon to Colorado.
  - I. aggregata candida*; eastern slope of southern Rocky Mountains and adjacent high plains.
- 2a. Ornithophilous *Diplacus*; red or salmon corollas.
  - D. puniceus*; coastal and insular southern California.
  - D. longiflorus*; chaparral hillsides in interior southern California.
- 2b. Sphingophilous *Diplacus*; pale lemon yellow corollas with long tube.
  - D. calycinus*; montane forest zone in central and southern California.
- 3a. Ornithophilous *Aquilegia*; nodding red and yellow flowers with stout nectar spurs.
  - A. formosa truncata*; Sierra Nevada and southern California mountains.
- 3b. Sphingophilous *Aquilegia*; ascending white flowers with long slender spurs.
  - A. pubescens*; Sierra Nevada crest.

## RESULTS

*Ipomopsis*. Hybrid swarms of ornithophilous *I. aggregata formosissima* × sphingophilous *I. tenuituba* occur at particular sites in northern Arizona (7), and hybrid swarms of ornithophilous *I. aggregata collina* × sphingophilous *I. aggregata candida* occur on the eastern slope of the Rocky Mountains in Colorado (6, 21). These populations contain one or both parental types, F<sub>1</sub> hybrids, and a complex array of hybrid segregates, recombination types, and backcross individuals.

One possible product of such hybrid swarms is variable hybrid intermediate populations that do not fit taxonomically into either parental taxon. Hybrid populations of this sort, derived from *I. aggregata collina* × *I. aggregata candida*, occur throughout a wide zone in the eastern slopes of the southern Rocky Mountains, Colorado. The populations segregate for flower color, corolla tube length, and other characters, with many or most plants in the intermediate range (6, 21). Both hummingbirds (*S. platycercus*, *S. rufus*) and hawkmoths (*H. lineata*) are frequent flower visitors. The birds and moths visit and cross-pollinate the various flower types freely (6, 8). All types in some study populations set seeds (8). This group of populations exemplifies the formation of a facultative hummingbird-and-hawkmoth pollination system in the progeny of ornithophilous × sphingophilous hybrids (selection course *iii* as outlined earlier).

Variable introgressive populations of *I. aggregata aggregata*, introgressed by *I. tenuituba*, are widespread in the

Wasatch Mountains, Utah, and Rocky Mountains, Colorado. These populations exhibit segregation for corolla color, corolla tube length, anther position, and other character differences between the parental species, but the variations are definitely skewed toward the character combination of the *I. aggregata aggregata* parent so that they fit taxonomically into that subspecies (7). These hybrid derivatives are ornithophilous; they represent selection course *i* in the postulated process.

There are two ecological races of *I. aggregata aggregata* in the Rocky Mountain region. A widespread race occurs at middle elevations in the Gambel oak–yellow pine zone up to about 8000 ft (2440 m) elevation. It has corolla tubes of moderate length (17–25 mm long). The second race occurs at higher elevations [ca. 8000–10,500 ft (2440–3200 m)] in the lodgepole pine and spruce–fir zones. In this race the corolla tubes are long (23–33 mm) (ref. 7; unpublished data). (The tube length measurements were made on dried specimens and are about 1 mm shorter than those for fresh specimens.)

It seems probable that the high montane race is a product of past introgression from subalpine *I. tenuituba* into the widespread mid-elevation race of *I. aggregata aggregata*. This would account for both its long corolla tubes and its ecological tolerance for high elevations. The populations are only moderately variable, suggesting that this race is a more or less stabilized product of introgression (7). The high montane race has ornithophilous floral characters and is known to be primarily hummingbird pollinated (22, 23). It apparently represents a more advanced stage of course *i* than that of the very variable introgressive populations described earlier.

Introgressive populations of *I. tenuituba* occur in scattered localities. Their flowers are sphingophilous as regards corolla tube length and width but not as regards corolla color, which ranges through various shades of pink (7). One such population in Sonora Pass, Sierra Nevada, was observed from the standpoint of flower visitors and pollinators during two flowering seasons. No hawkmoth visits were ever seen. Hummingbirds in the area paid no attention to the flowers in one year, but visited them occasionally and presumably pollinated them in the other year. The most reliable pollinator was a pollen-feeding melyrid beetle (*Trichochrous* sp.) (unpublished data).

There is no evidence at present that the floral variations in introgressive *I. tenuituba* are controlled by selection for hawkmoth visitations and pollination. Such evidence may turn up in future studies. On the other hand, the mechanisms of interspecific gene flow and hybrid segregation may be the dominant factors determining the variation pattern in introgressive *I. tenuituba*. In any case, *Ipomopsis* furnishes no known case of selection course *ii*.

*Diplacus*. *D. puniceus* of maritime habitats in southern California has typical ornithophilous flowers, and *D. calycinus* in the montane forest zone has sphingophilous flowers. The two taxa occur sympatrically in the Santa Ana Mountains, southern California, where their respective habitats interdigitate. But they exhibit a pattern of secondary intergradation along a broad transect from coastline to interior mountains in southern California. *D. longiflorus*, a second hummingbird-pollinated taxon in the chaparral zone of the interior foothills, forms a connecting link between *D. puniceus* and *D. calycinus*. Populations of *D. longiflorus* near the *D. puniceus* end of the transect show segregation for *puniceus* characters, while other populations near the *D. calycinus* end of the transect segregate for *calycinus* characters (10).

*D. longiflorus* is intermediate between *D. puniceus* and *D. calycinus* in vegetative and floral characters. It inhabits an intermediate ecological zone, the chaparral belt. Furthermore, this habitat and plant community are relatively recent,

whereas those of *D. puniceus* and *D. calycinus* have long been in existence. These lines of evidence suggest that *D. longiflorus* is a derivative of past hybridization between species similar to the present *D. puniceus* and *D. calycinus* (10). The hypothesis of a hybrid origin of *D. longiflorus* is consistent with the known frequency and importance of hybridization in *Diplacus* as a whole (10, 14).

*D. longiflorus* is hummingbird pollinated, as noted earlier (10, 19). The orange color of its corollas is unusual for western American hummingbird flowers, which are mostly red, but can be explained as a stabilized product of hybridization between red-flowered *D. puniceus* × lemon-yellow-flowered *D. calycinus*. Many facts about *D. longiflorus* point to the suggestion that it is another example of course *i* parallel to the high montane race of *I. aggregata aggregata*.

*Aquilegia*. In the Sierra Nevada, ornithophilous *A. formosa truncata* occurs along streams in coniferous forest up to 9000 or 10,000 ft (2740 or 3050 m) elevation, while sphingophilous *A. pubescens* occurs in fell-fields in the alpine zone from 9000 to 12,000 ft (2740 to 3660 m). The two species remain isolated in some areas of contact but hybridize in other areas.

A hybrid swarm near Saddlebag Lake north of Yosemite National Park has been studied in detail (1–3). In this area typical or nonintrogressive *A. pubescens* occurs on a rocky ridge in the alpine zone and typical *A. formosa truncata* occurs in the subalpine zone near one end of the ridge. The hybrid swarm grows on a small flat between the two species. The hybrid swarm grades into introgressive *A. pubescens* on the lower slope of the rocky ridge, which in turns grades into nonintrogressive *A. pubescens* on the upper parts of the ridge.

The nectar-containing floral spur has the following lengths in three subpopulations at Saddlebag Lake: typical *A. formosa truncata*, 10–17 mm; introgressive *A. pubescens*, 25–28 mm; and nonintrogressive *A. pubescens*, 29–40 mm. There is a continuous gradient over a relatively short distance in spur length—a short cline—from *pubescens*-like hybrid segregates to very long-spurred variants of *A. pubescens* (1). [The above measurements apply to dried specimens of the total spur, including both nectary and tube; the tube of a fresh spur, allowing for the size of the nectary and shrinkage during drying, is a net 1 mm shorter than the given lengths (15).]

Rufous and calliope hummingbirds freely visit *A. formosa truncata*, hybrid intermediates, and introgressive *A. pubescens* at Saddlebag Lake (1–3). The nectar at the base of the spurs is well within the reach of their bills and moderately extended tongues (15).

In the Saddlebag Lake site, hawkmoths (*H. lineata*) are frequent visitors and pollinators of *A. pubescens*, both the introgressive and nonintrogressive forms, and of *pubescens*-like hybrid segregates, but mainly shun *A. formosa truncata*. Hummingbirds also visit and pollinate *pubescens*-like hybrid segregates and introgressive *A. pubescens* (1–4). Hummingbirds may well visit nonintrogressive *A. pubescens* too, especially the shorter-spurred variants. We do not have good data as to just where in the spur length cline the hummingbirds phase out their visitations.

Nonintrogressive *A. pubescens* with spur lengths in a range of 29–40 mm is a marginal nectar source for western American hummingbirds. At the lower end of this range the basal nectar is accessible to hummingbirds but inefficient for them to extract, whereas at the upper end the basal nectar is inaccessible (15).

In the larger region that includes the Saddlebag Lake site, hummingbird foraging behavior on nonintrogressive *A. pubescens* is variable: the birds sometimes ignore these flowers, sometimes make occasional visits to them, and sometimes visit them regularly (2–4). In the latter case the birds may be obtaining upper nectar in the spurs. More detailed studies are needed to determine whether the variation in foraging be-

havior is correlated with spur length, bill length, and/or other factors. In any case, the variation in foraging behavior supports the conclusion that nonintrogressive *A. pubescens* is a marginal food plant for hummingbirds in its area.

Introgressive *A. pubescens* is widespread in the Sierra Nevada. It is a product of hybridization between ornithophilous and sphingophilous species which has become a facultative hummingbird-and-hawkmoth flower. It is another example of selection course *iii*.

## DISCUSSION

At the beginning of this paper I outlined three main courses of selection to be expected in the later-generation progeny of hybrids between an ornithophilous species and a sphingophilous species. Reversion to modified ornithophilous floral characters and a workable hummingbird pollination system is expected to occur where hummingbirds are the dominant flower visitors and pollinators (course *i*). The reciprocal case, course *ii*, involving reversion to a modified form of sphingophily, should occur where hawkmoths are the dominant pollinators. Reduction of the original specializations and change to facultative hummingbird-and-hawkmoth pollination would be expected in areas where both hummingbirds and hawkmoths are common and effective pollinators (course *iii*).

The alternative courses of selection depend on the relative amount of visitation and relative pollination effectiveness of the two types of pollinators. In my field experience I have found hummingbirds to be abundant, reliable, and active in most areas containing suitable flowers, whereas hawkmoth visitations are often less frequent and more erratic. However, quantitative estimates based on direct observations are not available and will be difficult to obtain. Both birds and moths show site-to-site and year-to-year variation in abundance. There is the further difficulty of comparing diurnal and nocturnal animals. We can, however, approach the problem indirectly.

The metabolic rate and calorie requirement for body maintenance are far higher in hummingbirds than in hawkmoths. In addition, female hummingbirds feed their nestlings, whereas hawkmoths do not provide parental care. In a typical nesting territory female hummingbirds forage on flowers from dawn to dusk. By comparison, *H. lineata* has an active flower visiting and feeding period during the first 3 or 4 hr of dusk and early evening, after which moth visitations become few and far between (24). Other hawkmoth species show a similar pattern (24). These considerations suggest that hummingbirds will normally exert a stronger selective pressure on flowers than hawkmoths, even where the two types of animals are equal in abundance.

A review of the evidence in three species groups yielded examples of course *i* in *Ipomopsis* and *Diplacus*, and course *iii* in *Ipomopsis* and *Aquilegia*, but no example of course *ii*. The bias in the set of actual examples is in agreement with expectations.

Course *iii* in *Ipomopsis* occurs in an area, the eastern Rocky Mountain foothills, where two sets of observers found much flower-visiting activity by both hummingbirds and hawkmoths (8, 22). Two sets of observers found the same situation in the high Sierra Nevada, where a case of course *iii* has developed in *Aquilegia* (1–3). Although we could not have predicted these two findings in advance, they come as no surprise in retrospect, since they occur in areas where both hummingbirds and hawkmoths are abundant and very active.

The courses of development outlined here may seem obvious when spelled out, but they have not been understood by previous workers. Elam and Linhart (8) carried out a study to test for floral isolation between ornithophilous and sphingophilous forms of *I. aggregata*, and did not find it. But they conducted their study in a hybrid zone where one should expect and does find facultative bird-and-moth pollination. The place to look for floral isolation is in other areas of the species group, where interspecific differentiation in floral characters is well developed (4).

The hypothesis of selection for floral characters and pollination system in the progeny of an ornithophilous × sphingophilous hybrid can be tested experimentally. Selection lines could be set up that are designed to yield end products corresponding to courses *i*, *ii*, or *iii*. Past experience with artificial selection in interspecific hybrid progeny suggests that the experiment would be successful. Segregating progeny of interspecific hybrids in plants respond rapidly to artificial selection for other traits. In *Gilia* (Polemoniaceae), a relative of *Ipomopsis*, the progeny of the hybrid *Gilia modocensis* × *Gilia malior* showed rapid response to artificial selection for vigor and fertility (25). There is every reason to believe that progeny of ornithophilous × sphingophilous hybrids would respond to artificial or natural selection for type of floral mechanism.

The long-term effects of hybridization and selection on floral isolation have been discussed in terms of the types of ornithophilous and sphingophilous pollination systems found in western North America. The conclusions can readily be extended to other combinations of parental pollination systems. The basic mechanisms outlined here should work in the same way in parental combinations and hybrid progeny of Old World ornithophilous and sphingophilous species, of bird-pollinated and bee-pollinated species, or of large-bee flowers and small-bee flowers, to name some other possibilities.

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