

Charles L. Argue

The Pollination Biology of North American Orchids: Volume 1

North of Florida and Mexico

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Preface

Orchids employ an amazing array of impressive strategies to achieve sexual reproduction. These strategies have intrigued biologists and amateur naturalists at least since Christian Konrad Sprengel (1750–1816) first associated the variation in orchid flowers with the attraction of pollinators. Since Darwin’s 1862 book, *The Various Contrivances by Which Orchids are Fertilized by Insects*, and especially in the past 50 years, a very large number of studies have revealed remarkable complexity and diversity in orchid–pollinator relationships. These studies comprise a vast literature currently scattered in numerous, often obscure, journals and books. *The Pollination Biology of North American Orchids* brings together, for the first time, a comprehensive treatment of this information for all native and introduced American orchids found north of Mexico and Florida. The book offers detailed descriptions and information on genetic compatibility, breeding systems, pollinators, pollination mechanisms, fruiting success, and limiting factors for each species. Distribution, habitat, and floral morphologies are also summarized. In addition, detailed line drawings emphasize orchids’ reproductive organs and their adaptation to known pollinators. All drawings are by the author, sometimes based on the published work of others, as indicated. Areas where information is limited are noted, thus spotlighting topics in particular need of further research.

The Pollination Biology of North American Orchids will be of interest to both regional and international audiences including the following:

- Researchers and students in this field of study who are currently required to search through the scattered literature to obtain the information gathered here.
- Researchers and students in related fields with an interest in the coevolution of plants and insects.
- Conservation specialists who need to understand both the details of orchid reproduction and the identity of primary pollinators to properly manage the land for both.

- Orchid breeders who require accurate and current information on orchid breeding systems. The artificial cultivation and breeding of native orchids is an important conservation measure aimed at reducing and, hopefully, eliminating the collection and sale of wild orchids.
- General readers with an interest in orchid biology. Technical terminology is kept to a minimum, and the text includes an introduction to concepts and terminology (Chap. 1) supplemented by brief parenthetical explanations of terms where they first appear in later chapters. An extensive glossary is also provided for the non-specialist reader.

Saint Paul, MN

Charles L. Argue

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Chapter 1

Introduction

Abstract The morphology of the orchid flower and the strategies orchids employ to attract pollinators are described. The types of breeding systems found in North American orchids are introduced along with the concept of pollinator syndromes and functional groups.

Keywords Breeding system • Pollinator syndrome • Functional group • Deceit • Mimicry • Magnet species • Competition • Pollinator attraction • Floral morphology

Orchid flowers and their pollinators provide many examples of highly specialized relationships. The plants are often fertile across species and even generic boundaries, and selection for reproductive isolation has led to the evolution of novel floral morphologies and pollinator behaviors. Biologists have devoted much effort to untangling the interactions between these flowers and their pollen vectors. Field and laboratory studies have now disclosed much about the pollination process, the breeding system, and the factors that limit or otherwise influence fruiting success in many species. Before discussing these findings, however, it is necessary to provide a very brief introduction to the general morphology of the orchid flower and the terminology used to describe orchid breeding systems and reproductive strategies. The ideas introduced here will be considered more fully below as they relate to specific orchid taxa. Readers interested in a more detailed introductory treatment should consult Arditti (1992), Dressler (1993), and Pridgeon et al. (1999). Those seeking a critical assessment of current concepts and techniques should begin with Glover (2007).

The Orchid Flower

Orchids are members of a large group of flowering plants known as monocotyledons. A basic feature of this group is the arrangement of flower parts in whorls of three. Although fundamentally true to this design, orchid flowers have diverged significantly from the basic monocot pattern. The extent and direction of this divergence can best be appreciated through a comparison of homologous floral parts in orchids and less specialized monocots. The basic pattern is evident in *Hypoxis*, a distant relative of the orchids. Here, all members of the perianth (the outer whorl of three sepals and the inner whorl of three petals) are alike in size, shape, and color (Figs. 1.1a and 1.2a). In contrast, the orchid perianth usually shows a high degree of differentiation. The dorsal sepal frequently differs from the others in size and shape and sometimes converges with the lateral sepals or petals to form a tube or bonnet of varying length (e.g. Figs. 9.1b and 12.1b). In others, such as the lady's-slippers (*Cypripedium*), the lateral sepals may partially or completely fuse with one another to form a single structure, the synsepal (Fig. 1.2b).

The median orchid petal, the lip or labellum, also typically differs markedly in size, shape, and often color from the other petals (Figs. 1.1b and 1.2b, c). Moreover, its orientation is often distinctive. In the early stages of flower development, it lies uppermost in erect inflorescences with the dorsal sepal positioned below, the customary orientation in monocots (as represented in Fig. 1.2b, c). But in mature orchids, it is usually lowermost in the flower (Fig. 1.1b). This position is usually achieved in North American orchids by a twisting of the flower stalk or ovary through an angle of 180°. The process is termed resupination, and the flower is said to be resupinate. In some species, rotation does not occur or proceeds through an angle of 360°, and such flowers are said to be non-resupinate.

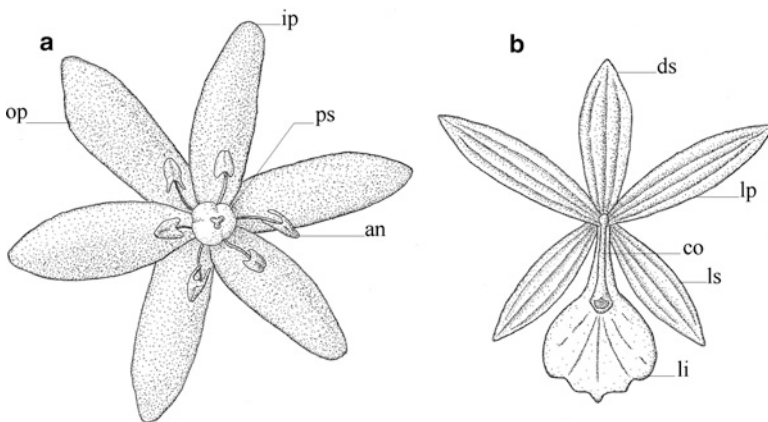


Fig. 1.1 (a) *Hypoxis* flower, (b) Generalized orchid flower. *an* anther, *co* column, *ds* dorsal sepal, *ip* inner perianth member (petal), *li* lip, *lp* lateral petal, *ls* lateral sepal. *op* outer perianth member (sepal), *ps* pistil

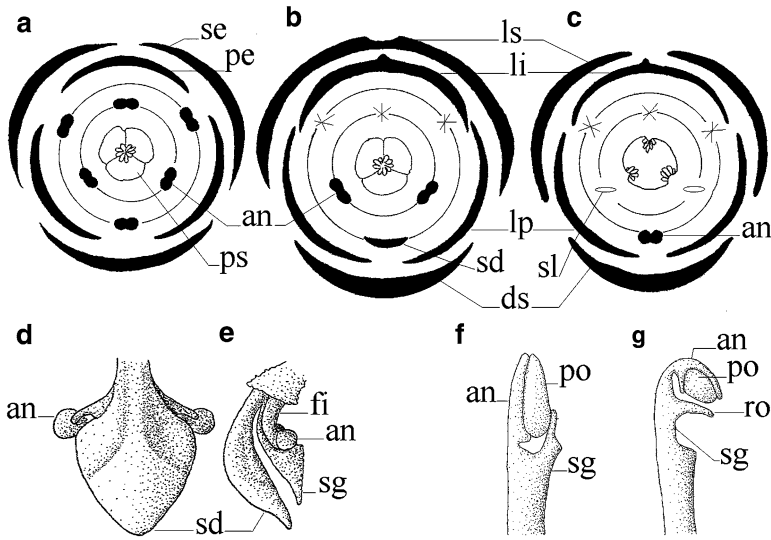


Fig. 1.2 (a–c) Floral diagrams. (a) *Hypoxis*; (b) Diandrous orchid; (c) Monandrous orchid; (d, e) Column of the diandrous orchid *Cypripedium fasciculatum*. (d) Top view; (e) Side view. (f, g) Columns of monandrous orchids. (f) Erect anther, side view; (g) Incumbent anther, side view. *an* anther (spore producing part of stamen), *ds* dorsal sepal, *fi* filament (stalk of stamen), *li* lip, *lp* lateral petal, *ls* lateral sepal, *pe* perianth member, *ps* pistil, *po* pollinium, *ro* rostellum, *sd* staminodium, *se* sepal, *sg* stigmatic area, *sl* stelia (small staminodia)

The most highly modified part of the orchid flower is a structure at its center called the column or gynostemium. The basic monocot pattern is represented as two whorls of three male organs, the stamens (bearing terminal sporangia or anthers). These surround a central female organ, the pistil (Figs. 1.1a and 1.2a). Alterations of this pattern in orchids include a reduction in the number of parts and a fusion of male and female components. In North American orchids, the column has either one or two functional anthers, and the orchids are accordingly said to be either monandrous or diandrous. The lady’s-slippers (*Cypripedium*) are diandrous (Fig. 1.2b, d). The two lateral anthers of the inner whorl in the basic monocot pattern (Fig. 1.2a) are retained (Fig. 1.2b), and a median anther of the outer whorl is modified to form a prominent shield-like element called the staminodium (Fig. 1.2b, d, e). The remaining anthers may be fused with the column or may be lost (Darwin 1862). Other North American orchids are monandrous, retaining only a single fertile anther at the apex of the column (Fig. 1.2c, f, g). The retained anther is homologous with the median stamen of the outer whorl in *Hypoxis* (Fig. 1.2a) and the staminodium in *Cypripedium* (Fig. 1.2b). The two lateral stamens of the inner whorl are sometimes visible as small staminodes (horns, wings, stelia, auricles) on the sides of the column (ellipses in Fig. 1.2c). As in diandrous orchids, rudiments of the remaining anthers may be variously incorporated into the structure of the column or lost altogether (see, e.g. Darwin 1862, Dressler 1993). The staminal or staminodial stalks, the filaments, are often united so completely with the pistil that the individual

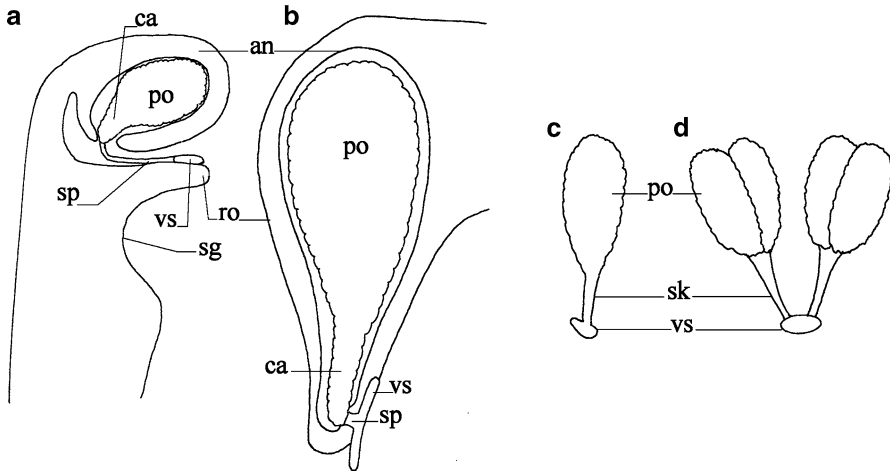


Fig. 1.3 (a, b) Columns, side view; (c, d) Pollinaria with one (c) and four (d) pollinia per viscidium. *an* anther, *ca* caudicle, *po* pollinium, *ro* rostellum, *sg* stigma, *sk* stalk, *sp* stipe, *vs* viscidium

components cannot be distinguished. However, in *Cypripedium* and some more advanced orchids such as *Spiranthes*, the union may be only partial (Fig. 1.2e) (Bonatti et al. 2006). The orchid stigma, a surface that receives the male gametophyte or pollen during pollination, is projected in *Cypripedium* (Fig. 1.2e) but is usually a shallow depression on the inner side of the column below and behind the anther in monandrous orchids (Fig. 1.2f, g). It is basically three-lobed although the lobes are fused and the median or dorsal lobe is often larger than the lateral lobes (Dressler 1993; Bonatti et al. 2006).

A morphologically variable structure that often forms a flap between the stigmatic surface and the anther is the rostellum (Fig. 1.2f, g). A number of functions have been attributed. Its positioning between the anther and stigma is thought to reduce or prevent accidental self-pollination. It may also display an adhesive surface, the viscidium (Fig. 1.3), which functions in sticking the pollen to a pollinator's body. In some cases, wounding of the rostellum during removal of the pollen also triggers ethylene evolution, which leads to senescence of the emasculated flowers (Avadhani et al. 1994). A viscidium is often reduced or absent in self-pollinating or primitive species such as *Cypripedium* or *Cephalanthera*.

The anther is essentially an elongated sac comprised of two to four locules or sporangia. This morphology is retained in primitive orchids but may be modified in advanced groups as, for example, the Epidendroideae, where the locules are sometimes transversely divided to produce eight pollen chambers. In other cases, the locules can be united in various ways or their development may be checked, leading to a reduction in their numbers and a reorientation of their partitions.

Anthers can be erect or incumbent (Fig. 1.2f, g). An erect anther is oriented parallel to the axis of the column and has the filament at its base as in many other monocots (Fig. 1.2f). This condition is considered relatively primitive and is found,

for example, in many Orchidoideae. An incumbent anther is bent downward (Fig. 1.2g) and is associated with a more specialized pollination strategy. In some less specialized members of the Epidendroideae, the transition can be observed during ontogeny (development of the organ during floral maturation), the anther being erect in the young bud but bending downward 90–120° as development proceeds to maturity (Dressler 1981). The incumbent condition is modified in various ways in advanced members of the Epidendroideae (Dressler 1981).

The anthers of most orchids do not produce particulate pollen grains as in most flowering plants but discrete pollen masses called pollinia (Fig. 1.3). Pollinia can bear an extension or stalk called a caudicle. This extension differentiates within the anther and is comprised of the remains of aborted pollen mother cells and possibly pollen grains and the tapetum (a layer of tissue lining the inside of the anther locule) (Rasmussen 1986). An extension of the caudicle that is derived from columnar tissue outside the anther in some specialized orchids is termed a stipe (Fig. 1.3a, b). There are two kinds of stipe (Rasmussen 1986). One, the tegula, is a plate developed from the dorsal epidermis of the rostellum; the other, the hamulus, is derived from an upwardly curved, distal extension of the rostellar apex. The caudicle or the stipe, if present, is usually attached to a sticky pad, the aforementioned viscidium, formed by the rostellum (Fig. 1.3). An easily ruptured, sac-like membrane, the busicle, which keeps the viscidium fresh and sticky, may cover it. The entire structure, comprising pollinia, stalk, and viscidium, is called a pollinarium (pl. pollinaria) (Fig. 1.3a–d). In animal-vector species that lack a viscidium, the pollen may attach directly to a sticky, stigmatic, or rostellar secretion, smeared onto the pollinator immediately prior to contact with the pollen.

In many orchids the basic structure of the anther with its four cells gives rise to the formation of four pollinia. In other orchids, the cells fuse in pairs resulting in a two-celled anther with two pollinia. However, pollinaria may include as few as one or as many as eight separate pollinia attached to a single viscidium (Fig. 1.3c, d). The flowers in many Orchidoideae produce two separate viscidia, each with a separate stalk and one or more pollinia.

Pollinia may be relatively uniform in structure or sectile. Sectile pollinia are comprised of numerous, small, loosely associated sub-compartments or packets of pollen, the massulae, within which pollen grains are variously interconnected (Zee et al. 1987; Dressler 1993). During pollination, individual massulae detach from the pollinium and a number may be deposited on each of a series of successively visited stigmas. In most orchids the pollen grains derived from a single pollen mother cell do not separate following meiosis but are structurally united by a partially shared pollen wall to form a group of four called a tetrad. However, the pollen grains are shed singly (as monads) rather than as tetrads in the subfamily Cypridarioideae and either as monads or tetrads in the subfamily Vanilloideae, in the tribe Cranichideae of subfamily Orchidoideae, and in the tribe Neottieae of subfamily Epidendroideae.

The texture of pollinia may be granular (soft) or hard and waxy. Granular pollinia are characterized by numerous intercellular spaces among the pollen grains, and individual grains may have well developed pollen walls. A relatively high ratio of

air to pollen wall surface refracts the light, and the pollinia appear more or less opaque. “Hard” pollinia have relatively little air space within the pollinium, and pollen walls are present only on the peripheral tetrads. Refraction is thus reduced and the pollinia appear translucent (Zavada 1990).

Pollen loads on individual stigmas can vary with the pollinator species, the size of the stigma, and other factors (Neiland and Wilcock 1995). However, very high loads, such as pollination with an entire pollinium, would routinely lead to much wastage of pollen: many massulae would fail to contact the stigma and would not germinate. Intermediate size loads, involving the deposition of a number of massulae rather than an entire pollinium, avoid this wastage while still providing high levels of pollen germination, maximum seed set, and some pollen tube competition to promote fitness among the progeny (e.g. Ottaviano et al. 1980; Neiland and Wilcock 1995).

The number of pollen grains produced and ovules or potential seeds contained in the ovary, the pollen to ovule (P:O) ratio, for massulate orchids such as *Platanthera*, *Galearis*, *Amerorchis*, and *Goodyera* is relatively low compared to outcrossing plants which do not have large pollen dispersal units. However, it is about double that seen in the Asclepiadaceae, which also have pollen grouped in pollinaria (Cruden 1977; Neiland and Wilcock 1995). In the latter, however, massulae are absent, and the entire pollinium is deposited into the stigmatic chamber. A low P:O ratio is therefore energetically efficient since a single pollinium cannot fertilize the ovules of more than one flower (Neiland and Wilcock 1995). In massulate orchids, on the other hand, where only a few massulae are usually deposited on any one stigma (e.g. Kevan et al. 1989; Neiland and Wilcock 1995), a higher P:O ratio increases the probability that a number of plants can be pollinated by pollen from the same pollinium (Neiland and Wilcock 1995).

Breeding Systems

Several breeding systems are present in North American orchids. Different breeding systems result in different levels of genetic recombination, a process that leads to offspring having different combinations of genes than their parents. This shuffling of genes is thought to have many advantages including an increase in adaptive potential and a reduction in the accumulation of deleterious genes. Many orchids are facultative and combine several breeding systems resulting in an increase in their reproductive versatility.

Self-Compatible Orchids

Self-compatible orchids are able to produce seed when a flower receives its own pollen or pollen from another flower on the same plant. If the pollen is transferred

from the anther to the stigma within a flower without the mediation of a pollinator and pollination is followed by fertilization of the ovules, the flower is said to be automatically self-pollinated and autogamous. If the process occurs while the buds are still closed, the flower is cleistogamous. If pollen transfer from the anther of one flower to the stigma of another results in fertilization, the process is called geitonogamy when the two flowers are on the same plant, cross-pollination (xenogamy, allogamy, or outcrossing) when on separate plants, and hybridization when on separate species. The potential levels of recombination and variation in the offspring range from low in autogamy and geitonogamy to high in cross-pollination.

Self-Incompatible Orchids

Self-incompatible orchids only produce seed if they receive pollen from a different plant, and fertilization in such a plant is therefore obligately xenogamous. Some species may just experience a reduction in seed number or viability when selfed and are therefore partially self-incompatible. Self-incompatible and partially self-incompatible plants may also suffer a reduction in capsule set or seed viability when restricted pollen and seed dispersal result in closely spaced plants receiving pollen from genetically related neighbors, an occurrence called biparental inbreeding. Various mechanisms tend to reduce the incidence of selfing in self-incompatible or partially self-incompatible plants. These will be discussed in connection with the breeding systems of individual orchid species.

Agamospermy (Apomixis)

Agamospermous orchids produce seed asexually. The embryos are derived wholly from maternal tissues, and no sexual recombination is involved. Like other breeding systems, agamospermy may be facultative and associated with varying levels of sexual reproduction.

General Attraction of Pollinators

Sexual reproduction in orchids is often limited by the availability or activity of pollinators. North American orchids employ a number of strategies to increase visitation. These will be elaborated in the sections dealing with individual orchid taxa, but in our flora usually involve general rewards, unique rewards, or deception (van der Pijl and Dodson 1966). Many offer nectar as a reward. Nectar usually contains a nutritious mixture of glucose, fructose, and sucrose along with some less common sugars and other substances. Composition of the mixture may be more or less constant for a given

species, and may, to some extent, reflect pollinator preferences (Cingle van der 1995). In addition to composition, nectar may vary in total sugar concentration as well as volume and time of secretion. Concentration and volume in a given orchid may vary with atmospheric pressure, relative humidity, and time of day.

Color, including ultraviolet, distinguishes flowers from their background and advertises a potential reward. Because the color vision of pollinators varies, flower color can be somewhat discriminating. Flower shape and fragrance also attract the attention of vectors. Flower color and shape provide long distance signals that insects can recognize (Kevan 1972). Floral fragrance can act either as a long or short distance advertisement, and in the latter case may prompt the pollinator to land and probe for nectar. Orchids may produce varying combinations of fragrant compounds, and these and their time of production may reflect a specific relationship between the orchid and its pollinator(s).

Some orchids provide no reward and attract pollinators by deceit. The mechanisms of deception include simulation of a food reward, mimicry of rewarding flowers, imitation of shelter or brood sites, rendezvous attraction, pseudoantagonism, and sexual deception. Non-rewarding flowers experience lower pollinator visitation rates and thus, lower levels of fruit and seed set. The evolution of deception has therefore proved to be something of an evolutionary puzzle. Since non-rewarding orchids comprise about one-third of all orchid species, it may be assumed, however, that this condition confers fitness advantages in some situations.

Two principal hypotheses have been advanced in an attempt to explain how deception could increase fitness. The first is that resources required for the production of a reward are limited and better reallocated to flower and seed production (Snow and Whigham 1989, Ackerman and Montalvo 1990). The second is that pollinators visit fewer flowers and spend less time on the inflorescences of non-rewarding plants, resulting in a decrease in geitonogamy and an increase in cross-pollination (Hodges 1981; Harder and Barrett 1995; Johnson and Nilsson 1999; Johnson et al. 2004). Other ideas have been proposed. Smithson and Gigord (2001), for example, in the study of a Mediterranean orchid, found that pollinaria were removed more frequently from nectarless plants. They argued that systems of deception evolved in response to a male function advantage. These hypotheses are reviewed in Jersakova et al. (2006) (see also Kropf and Renner 2008) and will be revisited below with reference to particular orchid species.

Not all the mechanisms of deception are found among North American orchids. Simulation of a food source (usually nectar but sometimes pollen) is the most common form of deceit in our flora and employs floral attractants, including flower shape, color, and scent, that pollinators associate with food. These may fit floral syndromes that typically attract a particular class of pollinators and may rely on newly emerged, inexperienced agents. Some pollinators are able to recognize scent more quickly than color (Bogdany 1978). Others may be more attuned to visual stimuli. Variation in floral odor or color might therefore function adaptively in reducing the rate at which the pollinators learn to recognize and avoid non-rewarding flowers (Ackerman 1986; Ackerman et al. 1997; Ferdy et al. 1998; Roy and Widmar

1999; but see Smithson et al. 2007). Variable flower color, for example, is sometimes associated with a lack of scent production, forcing the pollinator to rely on visual stimuli. However, variation, particularly in scent, can also occur in rewarding species, and the effect on the behavior of pollinators needs further study (Patt et al. 1989, Tollsten and Bergstrom 1989, Kaiser 1993).

Some deceptive orchids produce features that suggest a specific food source such as nectar guides or yellow hairs that simulate anthers or pseudonectaries (e.g. spurs) that produce no nectar (Gumbert and Kunze 2001, Galizia et al. 2005). Still others produce pheromones that elicit specific responses in the vector or structures, textures, and/or odors that suggest the presence of the vector's larval hosts. Characters may be differentially associated as part of an adaptive array to deceive the pollinator.

The flowers of deceitful orchids may also mimic the appearance of specific, sympatric flowers that provide a reward, and pollinators may visit the mimics by mistake. The subject of mimicry, as it applies to plants, remains controversial, and according to some workers, what appears to be mimicry represents an exploitation of evolved perceptual biases such as a pollinator's generalized preference for flowers of a certain size, shape, or color (Vereecken and Schiestl 2008, Schaefer and Ruxton 2009, but see Gumbert 2000). It seems difficult, however, to explain some forms of mimicry in these terms, as, for example, the evolution of flowers that attract male insects by simulating the appearance and odor (pheromones) of conspecific females.

It has also been debated whether either non-rewarding or rewarding plants occurring in a mixed population with other plant species that produce a reward are likely to experience improved pollination success as a result of an increase in the local abundance of potential pollinators, the so-called "magnet species effect" (Thomson 1978, Feinsinger 1987), or suffer reduced success as a result of increased competition for their services.

Johnson et al. (2003), for example, found significantly greater pollination success in Swedish plants of the non-rewarding orchid *Anacamptis morio* Bateman, Pridgeon, and M. W. Chase that were placed within clusters of nectar-producing plants compared to those placed outside such clusters (ca. 20 m away). The insects most likely to visit the orchid were those foraging on magnet species resembling the orchid in flower color and shape. When, as in this case, the orchid is a non-rewarding species, success generally requires that the magnet species be relatively more abundant than the mimic (Smithson and Macnair 1997, Ferdy et al. 1998, Johnson et al. 2003, cf Lammi and Kuitunen 1995). Smithson and Macnair (1997) and Ferdy et al. (1998) found that queen bumblebees quickly learned to avoid non-rewarding orchid flowers where they occurred in dense aggregations.

Interspecific facilitation of pollinators is also documented in mixed arrays of exclusively rewarding species. Duffy and Stout (2008), for example, found a positive relationship between the number of pollinator visits to the rewarding orchid, *Spiranthes romanzoffiana* Chamisso, and total floral density in mixed patches of this and other rewarding plants.

Where competition is a dominant factor, it might be to the advantage of the plant to bloom at another time or to grow at a remote site (Heinrich 1975, Boyden 1980,

Nilsson 1980, Dafni 1984, Firmage and Cole 1988). Mosquin (1971) suggested that natural selection would favor the evolution of earlier or later blooming dates in plants forced to compete for pollinators with other species producing plentiful resources. The frequently occurring pattern of early spring blooming in food-deceptive orchids, for example, has been considered an adaptive shift to secure pollination by newly emerged, naïve insects before the appearance of later blooming, rewarding species (Nilsson 1980; Internicola et al. 2008; but see Ruxton and Schaefer 2009 and Sietvold et al. 2010). Staggered flowering patterns can, however, reflect phylogenetic constraints or timing of resource acquisition or seed dispersal rather than competition among plants for pollinators (Johnson 1992, Johnson et al. 2003).

Lammi and Kuitunen (1995) obtained experimental evidence consistent with the so-called “remote habitat effect.” They found that the experimental addition of nectar-producing violet flowers to patches of the non-rewarding marsh orchid *Dactylorhiza incarnata* (L.) Soo reduced pollination success in the orchid, especially if the flower colors of the orchid and violet were a close match. However, in a similar experiment, Pellegrino et al. (2008) reported just the opposite. They set up patches of the non-rewarding orchid *Dactylorhiza sambucina* (L.) Soo and *Viola aethnensis* Parl. and found that competition only occurred when different color morphs were paired. When the color morphs of the orchid and violet were matched, the orchid appeared to benefit from the co-occurrence of the violet through floral mimicry and/or the magnet species effect, just as in the *Anacamptis morio* study. Internicola et al. (2007) obtained similar results using artificial flowers.

Competition and facilitation probably represent opposite ends of a continuum. The magnet effect might facilitate pollination at one time in a particular habitat, while earlier or later in the flowering season or at other sites with variable population densities and/or different plant species competition may predominate. Facilitation might, of course, also give rise to increased competition among members of the same species, leading to maximum seed set by those plants with the most attractive flowers.

Foraging insects only visit nonrewarding orchids or orchids in mixed arrays intermittently (Rathcke 1983; Stout et al. 1998). Such behavior can lead to reproductive interference, where the stigma may become clogged with heterospecific pollen, and pollen may be wasted through export to heterospecific stigmas (Free 1968, Waser 1983). This can be significant, but with regard to pollen receipt, orchid stigmas are wide and except for the introduction of pollinia from other orchid species, may be less likely than many other plants to suffer a lowering of reproductive success based on stigma contamination (Harder and Thomson 1989, Johnson and Edwards 2000).

The size of the plant population, the density of plants within the population, and the size of the inflorescence may also influence the attraction of pollinators. Studies that have investigated the impact of these variables on visitation rates and sexual reproduction in orchids have produced varying results. Once again, these will be considered below for individual orchid species.

Pollinator Syndromes in North American Orchids

Orchid flowers exhibit a complex of characters that tend to reflect adaptation to the morphology and behavior of their primary pollinator(s). The assumption is that co-evolution has led to the development of particular floral features that enhance the probability of attracting and exchanging pollen with certain pollinators or groups of pollinators. Differential combinations of floral characters are sometimes used to establish pollination classes or syndromes (Delpino 1868–1874, Faegri and van der Pijl 1971). The borders of the syndromes are not clearly demarcated, and a number of orchids attract a variety of visitors. In fact, Waser et al. (1996) and Waser and Ollerton (2006) believe that pollinator generalization may be the rule in the majority of plant–pollinator systems because variation in pollinator visitation levels and efficiency restrict the degree to which plants are able to specialize on single pollinators. Rather than focusing on single pollinators, however, Fenster et al. (2009) examined the effect of what they called functional groups (e.g. long-tongued bees, nocturnal moths etc.) and reported that about 75% of the plants they considered were adapted to a single functional group, sometimes including over 25 different species. They considered that it is the general morphological and behavioral characters of the functional group, rather than a particular pollinator species or taxonomic group, that exert selective pressure on floral evolution. If most flowers are adapted to functional groups, pollination syndromes have the potential to reflect, in a general way, a suite of reciprocal adaptations between the flowers and their pollinators. In addition to characteristics that attract certain pollinators, syndromes may also include features that exclude non-pollinating visitors. The following summary of pollinator syndromes is based largely on the classic works of van der Pijl and Dodson (1966) and Faegri and van der Pijl (1971).

Bee-Pollinated Orchids

Flowers that are primarily adapted to bee- or wasp-pollination are said to be melittophilous. About 60% of orchids fall into this category. Bee flowers typically have a well-developed landing platform with nectar guides or marks of contrasting color pointing the way to the nectary. The latter may or may not contain nectar. When present, the nectar occurs in moderate amounts and is usually more or less concealed. In some cases, the nectar guides reflect only ultraviolet light and are invisible to the human eye. The bee's visual spectrum is shifted toward the shorter wavelengths. Thus, it perceives ultraviolet as well as violet, blue, green, and yellow, but not red or orange, and bee flowers, usually brightly colored, appear to us to be blue, green, yellow, or white. However, some red or pink flowers contain ultra-violet absorbing pigments, which make them more attractive to bees. Bee flowers are open during the day, emit fresh and sweet odors, are often funnel or gullet shaped, and tend to be oriented horizontally. Pseudo-pollen may be present. Bee pollinators include both long- and short-tongued species, and nectar may accordingly be present in shallow or deep receptacles.