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The Pollination Biology of *Calypso bulbosa* var. *americana* (Orchidaceae): Initial Deception of Bumblebee Visitors

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Summary. The orchid Calypso bulbosa var. *americana* has deceptive flowers that provide no rewards for visitors. Near Banff, Alberta, the flowering period of this species is synchronized with the emergence of its pollinators, large bumblebee queens, in late spring. *Calypso* flowers appear to rely on the initial attraction and deception of newly-emerged naive bumblebees for pollination. Indirect evidence suggests that individual bees subsequently learn to avoid these flowers and that avoidance is learned quite rapidly. Avoidance behavior by pollinators is obviously detrimental to sexual reproduction in *Calypso*. This negative effect appears to be offset by the large number of seeds produced in plants which are effectively pollinated. A test of the hypothesis that *Calypso* flowers mimic flowers of the shooting star, *Dodecatheon radicatum* (Primulaceae) failed to provide evidence for mimicry.

Introduction

The Orchidaceae is the largest and most diverse plant family, with an estimated 30–35,000 species. In orchids, successful pollination results in fertilized ovules which can develop into hundreds, thousands, and even millions of seeds in a single seed capsule, depending on the species. Thus, the pollination of only a handful of flowers in a population may be enough to ensure the successful propagation of the species. This mode of reproduction is unusual among the flowering plants and may have led to the evolution of deceptive flowers in a large number of orchid species. Perhaps thirty percent of all orchid species provide no reward to floral visitors (Dodson, pers. comm.). Instead, they rely on deception for pollination. Although some orchids imitate the females or prey of floral visitors (e.g. *Trichoceros, Brassia*), the vast majority of non-rewarding orchids deceive visitors that search for food.

Deceptive flowers are of two general types. Simple deceptive flowers offer no rewards for floral visitors. Mimetic flowers offer no rewards either and the flower or part of the flower imitates a particular plant, animal, or structure such as a food body. Both types deceive floral visitors which serve as vectors in pollination. The adaptive significance of deception is that plants with deceptive flowers do not produce costly food rewards needed by most other species to attract visitors for pollination.

Floral deception involves reproductive gambling for a plant species. The continued visitation by pollinators and, consequently, the reproductive success of a plant which offers consistent, high quality food rewards is fairly certain once it is discovered by floral visitors. The reproductive success of a deceptive plant species, on the other hand, is dependent on how well floral visitors are deceived. At any time a particular floral visitor may discover the ruse and abandon the plant, or simply fail to continue to visit it because no rewards are provided. A plant may be abandoned before or after pollination has taken place. Thus, species with deceptive flowers may risk reproductive failure and may face local or species extinction.

In the one-hundred thirty or more species of North American orchids, pollinia are generally carried from flower to flower by insects. Most North American orchids with deceptive flowers are pollinated by bumblebees. These include members of the genera *Arethusa, Calopogon, Cypripedium* and *Calypso* (Stoutamire, 1971). In most cases, the relationships between the bees and the orchids are poorly understood. Recently, much attention has been focused on the pollination biology of *Calypso bulbosa* L. Mosquin (1970, 1971), Stoutamire (1971) and Ackerman (1981) have made some important ecological investigations of this species. The purpose of this paper, therefore, is to provide some additional information on; the population and pollination-biology of *C. bulbosa;* the extent to which bumblebee visitors are deceived by Calypso flowers or learn to avoid them; and the hypothesis of Mosquin (1970) that flowers of this species mimic those of the shooting star, *Dodecatheon radicatum.*

Description of the Species and the Study Areas

Calypso bulbosa L. is a circumboreal species. Four distinct varieties of this orchid exist; var. *bulbosa* in Eurasia, var. *japonica* in Japan, var. *occidentalis* (Holz.) in the Pacific Northwest of North America, and var. *americana* (R. Br.) which occurs from the Rocky Mountains eastward in North America. Ackerman (1981) studied var. *occidentalis* in California, while Mosquin (1970, 1971) studied var. *americana* in two areas near Banff, Alberta, Canada.

The present study was conducted on var. *americana* in the same two localities where Mosquin (1970) made his studies. One study site was located at Johnston's Canyon,

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24 km. WNW of Banff. A second site was located at Mt. Eisenhower, 32 km. WNW of Banff. Data were collected from 12–20 June, 1977.

In the Banff area, *Calypso bulbosa* var. *americana* can be found in moist, shady coniferous forests with mossy groundcover. *Calypso* is a perrenial and produces a single ovate leaf from an underground corm in the fall. The plants remain in this condition over winter. In the spring, each plant produces a single flower. In late summer the plants become dormant, the single leaf withers, the fruits dehisce, and the thousands of minute seeds contained in the seed capsule are dispersed by the wine.

Calypso flowers are showy and slipper-shaped, and have rose-pink sepals and petals. They have a strong, perfume-like fragrance when fresh. The lamina of the lip of var. *americana* is yellow with a few large reddish spots and is adorned with several rows of yellow hairs. The saccate portion of the lip has alternate white and rose-pink stripes. At the base of the labellum are double 'nectar spurs' which are deceptive structures, since the flower produces no nectar. The broad, arched column is also rose-pink and forms a hood over the lip. The operculate anther containing the pollinarium is located on the underside of the column, just in front of a small ridge, and is covered by a small cap. The anther is deciduous and can be removed with slight effort or pressure. The stigma is located on the column, just behind the anther.

Plants of *C. bulbosa* bloom in the equivalent of late spring at their respective altitudes and latitudes. Reproduction is by both sexual (cross-pollination) and asexual (vegetative) means. Asexual plantlets are generally spread by coralline rhizomes which grow from a single tuber. The flowering period of var. *americana* in the Banff area was determined by Mosquin (1971) to extend from approximately 30 May – 21 June. Flowering occurs during the period when bumblebee queens are actively foraging for nectar and pollen in order to start their colonies. Bumblebees are the only known insects which serve as vectors for cross-pollination in *Calypso*.

Pollination by Bumblebees

In order to obtain information concerning the extent of bumblebee visits to *Calypso* flowers, and the extent to which these insects avoided or were deceived by these flowers, it was necessary to gather indirect information, since flower-visits by bumblebees occurred too infrequently to be observed directly. Data on visitation were obtained by capturing bumblebees at the Mt. Eisenhower site, mounting them and examining them under a dissecting scope. Counts were made of pollinaria, and viscidia, the sticky discs by which the pollinaria adhere to the pollinator. In the case of the *Calypso* pollinarium, the viscidium adheres to the well-protected hairless dorsal crevice of the thorax between the thorax and abdomen of the bee (scutellum). When the pollinarium comes off, the viscidium remains behind, firmly attached to the cuticle of the bee. Thus, pollinaria and viscidia provide a record of a bee's activity. By counting intact pollinaria and viscidia on bees, the number of *Calypso* pollinaria a bee was carrying or had carried during that season could be determined. The position of pollinaria the scutellum of bees and the effectiveness of the natural adhesive of the viscidium make it highly unlikely that a bee could remove them by grooming. Consequently, in the discussion that follows, bees bearing viscidia are assumed to have given up their pollinia to *Calypso* flowers.

The probable sequence of events in the pollination of *C. bulbosa* by bumblebees has been described by Stoutamire, Mosquin, Ackerman, and Gumprecht (1977). A foraging bumblebee queen, flying in the vicinity of a *Calypso* flower orients itself in front of the labellum of the flower and alights. After searching in vain for pollen, the bee pushes its head and thorax under the column of the flower and probes the deceptive nectar spurs at the end of the labellum for nectar. Finding nothing, the bee backs out of the flower.

For attachment of the pollinia to occur, the bee must be of the right size, so that the winged column of the flower fits the insect's thorax closely. The bee must also enter the flower deeply and back out with an arched body so that the edge of its scutellum contacts the viscidium, cementing the pollinarium to the bee. When backing out of a flower, the bee first brushes the stigma where it may deposit pollinia already on its scutellum, and then the anther cap and pollinarium of the flower are removed.

Bumblebee Behavior, Learning and Memory

The flowering periods of most bumblebee-pollinated spring flowers in the Banff area are only a few weeks long (Mosquin 1971). Since bumblebee queens in temperate climates live only one year (Heinrich 1979), these initially naive bees have only a short time in which to exploit flowers of a given species for their pollen and nectar rewards. Thus, there should be strong selection in bees for the ability to assess a variety of flower types and quickly determine which types are most profitable in terms of the rewards they offer for a given amount of foraging time. It follows that bees should avoid unprofitable or deceptive flowers. Heinrich (1979) found that naive bumblebees chose flowers more or less indiscriminately on their first foraging trips. They visited flowers with no nectar or pollen rewards, as well as those with ample rewards. However, after two to six foraging trips, most of the bees were expert foragers and had specialized on the plant species in the area which, based on each bee's experience, yielded the most profits in the shortest time. Each bumblebee appeared to arrive at its choice of flower independently.

In order to distinguish one type of flower from another in a complex environment, and to discover what flowers are worth visiting, bees must have a memory and the ability to learn. To my knowledge, no laboratory experiments on learning by bumblebees have been conducted to date. However, some excellent work has been done on honeybees (*Apis mellifera*). In 1910, Karl von Frisch established that honeybees could see and differentiate colors and that they could learn to associate colors with food rewards. Menzel and Erber (1978) showed that even though honeybees function as strongly-programmed behavioral machines, their mechanisms of learning and memory are not unlike those of higher animals. Honeybees have short-term and long-term memories like vertebrate species. In Menzel and Erber's short-term memory experiments, bees showed one-trial learning. When tested immediately after learning (0–12 min), they chose a previously rewarded color with a high degree of accuracy (80%). In long-term memory experiments, bees rewarded three times on a particular color showed an initial high degree of accuracy in choosing a rewarded color

(75%), with the accuracy decreasing and nearing the level of spontaneous choice (54%) after about six days. Thus, after initial learning, reinforcement of memory may be necessary for bees to attain a high degree of accuracy in choosing rewards. It is assumed for purposes of discussion here that the process of learning and memory formation is similar for honeybees and bumblebees.

Results and Discussion

Both Mosquin (1970) and Ackerman (1981) found that flowers of *C. bulbosa* were self-compatible, but that in nature this species was an obligate outcrosser and was entirely dependent on bumblebees for pollination. Although bumblebees are the only known pollinators of *Calypso,* none were observed visiting *Calypso* flowers during the course of this study even though I watched groups of flowers for up to several hours at a time. Bumblebee visits to *Calypso* are rare in space and time, Mosquin (1970), Stoutamire (1971), and Ackerman (1981). Mosquin also did not observe any bumblebees visiting *Calypso* in his study. Ackerman (1981) observed several bumblebees visiting *C. bulbosa* var. *occidentalis,* but all were too small to effect pollination. Wollin (1975) watched *Bombus pascuorum* visit *C. bulbosa* var. *bulbosa* in Sweden.

The bumblebees captured at Mt. Eisenhower and Johnston's Canyon were primarily queens of two species, *Bombus melanopygus* (Nyl.) and *Bombus bifarius nearcticus* (Handl.). A few queens of *Bombus occidentalis* (Grne.) were also captured. In addition to the queens, I caught several small worker bees of *B. melanopygus* and *B. bifarius* but none of them carried *Calypso* pollinaria or viscidia. Consequently, I concluded that bumblebee workers were generally too small to be effective pollinators. Ackerman (1981) drew the same conclusion after watching one small bee (*Emphoropsis miserabilis*) visit six flowers of *C. bulbosa* in succession. The bee was ineffective in removing pollinaria from any of these flowers.

Of the 843 *Calypso* flowers I examined, 87% showed no evidence of visitation by bumblebees, while 12% had pollinaria missing, indicating that the flowers had been visited by bees. Only 1% of the flowers had been pollinated, as determined by the presence of a pollinium on the stigma of the flower. Deception of floral visitors by *Calypso* flowers appears to result in a very low level of pollination. Since deceptive orchids generally have a low percentage of pollination and hence a low seed set (Ackerman 1975; Dafni and Ivri 1979; Thien and Marcks 1972) populations of *Calypso* in Banff are no exception to this general rule.

My data on pollination correspond closely with those of Mosquin (1970) who examined *Calypso* populations in the same localities in 1968. He found that 88% of the flowers sampled (N = 1654) had not been visited by bees and 12% had pollinia that were either dislodged, missing or attached to the stigmas of the flowers.

The data in Table 3 show how many bees captured at random at the Mt. Eisenhower site carried *Calypso* pollinaria or viscidia. Fifty-seven percent of the bees showed evidence of having visited flowers of *C. bulbosa* at least once, while 43% apparently had not visited *Calypso* flowers. Although over half of the population of initially naive newly-emerged queens sampled appear to have had experience with *Calypso,* the low percentage of pollination observed (1%) provides indirect evidence of rapid avoidance learning by bees. The term avoidance as used here is synonomous with 'failure to visit'. The mechanism is probably quite different from the negative conditioning learned by some animals as a result of a bad experience (e.g. as in the case of a predator that encounters distasteful prey; Boyden 1976). Rather, the lack of reward in *Calypso* flowers probably results in a lack of reinforcement for the bee to continue to visit the flowers. The tendency of bumblebees to exhibit flower constancy behavior while foraging (Heinrich 1979) should also result in their visiting *Calypso* flowers less often than the number of times they are encountered in the environment. Some bees (including the 43% above?) would become rapidly conditioned to visit other flowers without having visited *Calypso* at all.

Mosquin (1970), Stoutamire (1971) and Ackerman (1981) all concluded that naive bumblebee queens probably learn to avoid *Calypso* flowers after one to a few trials. Data of mine which also support this idea include (1) Seventy-nine percent of the bees captured with pollinaria or viscidia carried only one pollinarium or visicidum. (2) None of the bees captured carried more than three pollinaria. (3) Only 10% of the flowers which showed evidence of visitation had been pollinated. (4) No bumblebees were seen visiting *Calypso* flowers, even though many hours were spent observing groups of flowers. (5) *Calypso* flowers and bumblebees were quite common in the two study areas.

Sexual reproduction appears to account for the general abundance of *Calypso* in the Banff area. My estimates of the density of this species at Mt. Eisenhower and Johnston's

Table 1. Distribution of flowers of *C. bulbosa* var. *americana*

Area	1 flower	2 flowers	3 flowers	≧4 flowers
No. of clumps with				
Johnston's Canyon	85	37	24	33
Mt. Eisenhower	36	19	15	36
No. of flowers in clumps				
Johnston's Canyon	85	74	72	207
Mt. Eisenhower	36	38	45	286
Totals	121	112	117	493

Table 2. Pollination of flowers of *C. bulbosa* var. *americana*

	No. of fls. with original pollinarium intact	No. of fls. with original pollinarium missing	No. of fls. with new pollinia present on stigma	Total no. of fls. examined
Johnston's Canyon	388	46	4	438
Mt. Eisenhower	344	55	6	405
Total	732	101	10	843

Table 3. Pollen loads of queen bumblebees captured at Mt. Eisenhower

Pollinaria	1 Calypso pollinarium	2 Pollinaria	3 Pollinaria	≧4 Pollinaria
No. of bees with	36	12	2	0
Viscidia	1 Calypso viscidium	2 Viscidia	≧3 Viscidia	1 Viscidia, 1 pollinaria
No. of bees with	40	4	0	2
Total no. of bees with pollinaria or viscidia	96		Total no. of pollinaria on bees	68
Total no. of bees w/o pollinaria or viscidia	72		Total no. of viscidia on bees	50

Canyon (18 plants/acre) roughly agree with those of Mosquin (1970). During the sampling period in which this study was conducted, *Calypso* was by far the most abundant woodland wildflower. For a further discussion of plant species composition in these sites see Mosquin (1971).

The data in Table 3 also show that pollinia transfer from bee to flower is far from totally effective. Forty bees carried only one viscidium. Although they may have pollinated a subsequent flower after picking up a pollinarium on an initial flower, they failed to pick up a new pollinarium on the flower where they delivered the pollinia. Twelve bees carried two intact pollinaria. Though they must have visited at least two flowers, they failed to pollinate a second or subsequent flower. Two bees carried three intact pollinaria.

As Ackerman points out, although the pollination mechanism in *Calypso* is, in general, specific for one type of floral visitor, pollinium deposition and pollinarium removal are not guaranteed consequences of any given visit by a pollinarium-laden bee. This statement is verified by my data. Excluding bees carrying only one pollinarium (in which it is assumed that they had visited only one flower) in only two instances (bees carrying one pollinarium and one viscidium) out of a total of sixty does the mechanism for pollen transfer appear to have been totally effective. Thus, the pollinator-flower fit is imprecise. Two factors account for this lack of precision. First, pollinator size is variable. Second, the size of *Calypso* flowers is variable, hence the throat of the lip and the fit of the column to the bee is variable. Since bumblebee size is probably dependent on nutrition (Heinrich 1979) and flower size in *Calypso* appears to be dependent on nutritive and growth factors, it is unlikely that the pollinator-flower fit could evolve to become more precise, or that the amount of error in the mechanics of pollination could be reduced by some type of selective floral evolution.

Several flowers examined were in shreds, presumably the result of a bumblebee entering a flower too far, becoming trapped and then fighting or chewing its way out. Although *Calypso* flowers are deceptive, they are certainly not similar to trap flowers which entomb floral visitors and then allow them to exit only via certain passageways or after the pollen has been shed and the barrier organs have wilted (Meeuse 1961).

The strength of the odor in *Calypso* flowers appears to be related to the age of the flower. Older flowers (2–3 wks. old) had little scent, while fresh ones had a strong fragrance. This may explain the discrepancy in the literature on the odor of these flowers with some researchers claiming the flowers are scentless, and others claiming they are strongly scented.

The Mimicry Hypothesis

Although most researchers consider *Calypso bulbosa* to be a flower of the simple deceptive type, Mosquin (1970) noted that several bumblebee species which were carrying *Calypso* pollinaria were visiting another pink-flowered species, *Dodecatheon radicatum,* which was not particularly common in the region and from a distance looks superficially similar to *Calypso.* He thought that the bees, accustomed to obtaining pollen from *Dodecatheon,* might have become conditioned to respond to pink flowers, and hence might mistake *Calypso* flowers for *Dodecatheon* flowers. He also noted that the flowering period of *C. bulbosa* near Banff (30 May–21 June) coincides rather closely with that of *D. radicatum* (28 May–14 June). Mosquin hypothesized that *Calypso* flowers, which offer no rewards to visitors, might mimic *Dodecatheon* flowers which offer ample rewards to visitors.

To test his hypothesis, I obtained data on the habitats of both *Calypso* and *Dodecatheon,* studied the foraging behavior of bumblebees visiting flowers of *Dodecatheon* and collected two groups of bumblebees at the Mt. Eisenhower site. The first group of bees was collected while visiting flowers of the alleged model species, *D. radicatum,* which was the only abundant *Dodecatheon* species in the area. The second group of bees was collected while visiting flowers of species other than *D. radicatum* (Table 4). My working hypothesis was that if *C. bulbosa* was indeed a mimic of *D. radicatum,* then bees visiting and captured on *D. radicatum* would have confused the two species more often and would, in general, carry more *Calypso* pollinaria than bees captured on other types of flowers.

The data in Table 4 show a test of the mimicry hypothesis. Of the bumblebees captured while visiting flowers of *D. radicatum,* 49 carried *Calypso* pollinaria or viscidia and 37 did not. Of the bees collected on other flowers or flying free, 47 bore *Calypso* pollinaria or viscidia while 35 did not. These data reveal no significant difference in the number of bees carrying pollinaria or viscidia in the two groups. Thus, the limited data presented here support the null hypothesis, i.e. that *Calypso* is not a mimic of *Dodecatheon* and that bumblebees can distinguish between these two species.

Table 4. Bumblebee queens captured at Mt. Eisenhower while visiting *D. radicatum* flowers (Group 1) or visiting other flowers and flying free (Group 2)

Group 1	1 Calypso pollinarium	2 Pollinaria	3 Pollinaria	≧4 Pollinaria
No. of bees with	20	5	1	0
	1 Calypso viscidium	2 Viscidia	≧3 Viscidia	1 Viscidia, 1 pollinaria
No. of bees with	20	2	0	1
Group 2	1 Calypso pollinarium	2 Pollinaria	3 Pollinaria	≧4 Pollinaria
No. of bees with	16	7	1	0
	1 Calypso viscidium	2 Viscidia	≧3 Viscidia	1 Viscidia, 1 pollinaria
No. of bees with	20	2	0	1
	Group 1	Group 2		
Total no. of bees with pollinaria or viscidia	49	47		
Total no. of bees w/o pollinaria or viscidia	37	35		

Differences between *Calypso* and *Dodecatheon* which might lead to the recognition of these species as separate by bumblebees include (1) Habitat differences. *Calypso* and *Dodecatheon* occur in distinctively different habitats, although they sometimes were found as little as a few hundred feet apart. *Calypso* grows in damp coniferous forests which generally get little light or sun, while *D. radicatum* is usually found in open, grassy country. (2) Floral odor. Although the color of *Dodecatheon* and *Calypso* flowers in quite similar, *Dodecatheon* flowers have a distinctively different odor from *Calypso* flowers which bees may recognize. (3) Foraging behavior of bees. Bumblebees visiting flowers of *Dodecatheon* exhibit a specialized type of foraging behavior when collecting pollen. They vibrate their wings while on the flower (making a buzzing sound) to shake loose pollen which is hidden in the flower. Bumblebees do not exhibit this type of behavior when visiting *Calypso* flowers (Ackerman 1981).

Both Heinrich (1979) and Ackerman (1981) observed that bumblebees with floral preferences may, at a distance, mistake the similarly-colored flowers of one species for another. However, such mistakes are generally short-lived because bees veer away on closer inspection where floral odor comes into play. Although bees may, at a distance, mistake *Calypso* for *Dodecatheon,* the overall resemblance between these two species would probably have to be much more finely-tuned for bumblebees to be lured for complete successive visits.

Floral Deception

In some cases, floral deception may be so effective that visitors are deceived over and over again and continue to visit a plant which offers them nothing (e.g. *Ophrys:* Kullenberg and Bergstrom 1976). In other cases, however, where the deception is less good, floral visitors may learn to avoid the flowers of a given species rapidly, resulting in a low incidence of pollination. While highly effective deceptive flowers would require that only a few floral visitors be deceived continually to result in a high incidence of pollination for a given plant population, poor or ineffective deceptive flowers would require that a large number of naive individuals constantly be recruited to counter the effect of avoidance learning. The latter situation appears to be the case with *Calypso.*

Floral mimicry should enhance the advantage gained by simple deceptive flowers. As a result, some types of simple deceptive flowers should eventually evolve to become mimetic. Heinrich (1979) cites an interesting example of an orchid which may have initially had simple deceptive flowers and later evolved mimetic flowers. The orchid is the grass pink, *Calopogon tuberosus* (=C. pulchellus), which occurs in the eastern U.S. and Canada. The flowers of this orchid provide no food rewards, and are large, conspicuous and showy. According to Heinrich, they are visited by searching bees (primarily *Augochlora*) that are sampling the available flowers and have not yet established their foraging specialties. On one occasion, Heinrich watched 14 bumblebees visit 75 *Calopogon* flowers. Another time, he watched one bumblebee visit 17 *Calopogon* flowers in succession before losing sight of it.

Calopogon flowers are deceptive in several ways, and this reduces their chances of being quickly identified by the bees. First, they are unscented. Since bees normally rely on scent for close-in orientation and identification of flowers, they are forced to rely heavily on color to recognize these flowers. Secondly, they are variable in color. Most of the plants examined by Heinrich had bright pink flowers, but there were all gradations from white to purple. Color variability poses a problem to bees. A bee might learn to identify and avoid unrewarding *Calopogon* flowers of a particular color, but would still be presented with a confusing array of flowers of different colors. The third deceptive tactic in the grass pink's repertoire is mimicry. The pink-flowered individuals of *Calopogon* appear to mimic those of another pink orchid, the rose pogonia (*Pogonia ophioglossoides*) which offers nectar. The grass pink's flowers also have strong ultraviolet reflectance patterns, like those of the rose pogonia. The two species are found in the same habitat and bloom at the same time of year.

Although *Calypso* flowers, like those of *Calopogon,* lack food rewards, they do not appear to possess any of the additional deceptive features that are found in *Calopogon,* such as variability in color, lack of scent, or mimicry of another species that offers food rewards – characteristics that would confuse pollinators and cause them difficulty in identifying flowers, resulting in a higher frequency of visitation and pollination.

Vogel (1978) suggested that the flowers of several nectarless genera of orchids resemble a kind of pollen flower through pollen imitation. In *Calopogon, Pogonia, Arethusa, Oncidium,* and other genera, yellow hairs, mostly on the labellum, appear to function as pollen dummies. Flowers of *C. bulbosa* var. *americana* and var. *bulbosa* also possess yellow hairs on the labellum which may function in a similar manner. Gumprecht (1977) claims that *C. bulbosa* var. *bulbosa* are doubly-deceptive. He states that naive bees visiting the flowers are first deceived by the quasi-stamens and secondly by the false nectar spurs. This is certainly a plausible hypothesis. However, since most researchers have not observed bumblebees directly on *Calypso* flowers, this must await further observation. If varieties *americana* and *bulbosa* are deceptive pollen flowers, it would be interesting to see if they are any better at attracting or deceiving bumblebees than other varieties of this species (e.g. var. *occidentalis*) which lack yellow hairs on the labellum.

Forgetting by bees, and the need for reinforcement of memory after initial learning (as suggested by the experiments of Menzel and Erber) may be of benefit to plants with deceptive flowers and result in a greater incidence of pollination. Species such as *Calypso bulbosa* may benefit from this lapse of a bee's memory. However, in nature, the rate at which a bee forgets might be less than that indicated by laboratory experiments. Real flowers are three-dimensional and have a distinct color (often with honeyguides), shape, and sometimes odor, whereas the colored paper and light-illuminated glass discs used in laboratory experiments are two-dimensional and lack other characteristics which bees might use to identify them. Thus, the combined cues of flowers in nature might result in fewer errors by bees and less forgetting (i.e. better reinforcement of memory) once a bee has approached a flower.

Stoutamire (1971) hypothesized that bumblebees are attracted to *Calypso* flowers because of the latter's conspicuous coloration. Although many types of flowers might be considered to be conspicuous, little attention has been given to the study of conspicuousness in flowers and the initial attractiveness of different types of flowers to naive visitors. It is possible that the conspicuous, showy flowers of *Calypso* might be initially more attractive to naive bumblebee visitors than many of the other spring-flowering species growing in the same geographic area.

In the same paper, Stoutamire suggested that avoidance learning by bees might prevent some orchids from developing large populations, and that the rarity of the flowers would, in turn, limit a bee's contact with them and hence its ability to develop avoidance reactions to them. He claimed that such a feedback mechanism controlling population size might have positive survival value for species with deceptive flowers such as *C. bulbosa.* Although this feedback mechanism could be operating with small populations of *Calypso* elsewhere, this species is too abundant in the Banff area for such a mechanism to be operating.

In a species with deceptive flowers, it would be interesting to compare seed set in two experimental groups; a group of flowers in which artificial nectar rewards were added on a consistent basis, and a control group with normal deceptive flowers (lacking nectar). In this way, the effect of food rewards on visitation frequencies and pollination by bees and the cost of deception might be measured. Ackerman (1981) attempted to do this, but I do not consider the results of his experiments to be conclusive for the following reasons. First, he injected a weak sugar solution (10% sucrose) into *Calypso* flowers in the wild. Baker (1975) has shown that the average sugar concentration of most bee flowers is about 35%, and in some cases may reach a level as high as 70–80%. Thus, Ackerman's sugar solution was probably too dilute to effectively simulate nectar found in a normal bee flower. Second, he injected sugar solutions into flowers about once a week. Since most bee flowers produce nectar on a daily basis, artificial nectar should probably be added to flowers more frequently. I plan to conduct future experiments of this type on populations of *Calypso* in the Pacific Northwest.

Conclusions

My data appear to support the following conclusions about *C. bulbosa* var. *americana* and its bumblebee visitors. (1) The flowering period of this species appears to be synchronized with the emergence of large bumblebee queens in late spring. This synchronization is significant since worker bees are generally too small to be effective pollinators. (2) *Calypso* flowers rely on the initial attraction of bumblebees to a few flowers of seed set, with individual bees then apparently developing avoidance reactions to the flowers. (3) The abundance of *Calypso* plants in the Banff area probably serves to reduce the overall effectiveness of deception in this species because bees encounter many plants, frequently. This situation would lead to rapid avoidance learning by bees and frequent opportunities for reinforcement of this learning. (4) Bees captured on *Dodecatheon radicatum* flowers showed no greater incidence of having visited *Calypso* flowers than did bees captured on other types of flowers or flying free. Thus, *Calypso* flowers do not appear to mimic those of *D. radicatum.* (5) Few pollination events occur even though bumblebee queens may be common in the immediate vicinity of an area with many *Calypso* flowers. (6) Bumblebee queens appear to cease visiting *Calypso* flowers after one to a few trials, as determined by the number of *Calypso* pollinaria or viscidia bees were carrying and the low frequency of *Calypso* flowers pollinated (1%). Consequently, *Calypso* flowers appear to rely on the initial attraction and deception of naive bumblebees for pollination.

Avoidance behavior by pollinators is obviously of negative value to the orchid species as a whole, but this appears to be offset by the high reproductive yield (thousands of seeds) in plants which are effectively pollinated and favorable conditions for germination and growth, leading to large populations of *Calypso* in the Banff area. Although the flowers of *C. bulbosa* are not highly effective in deceiving bumblebee visitors, these other factors appear to ensure the reproductive success of the species.

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