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EFFECT OF POLLINATION SUCCESS ON FLORAL LONGEVITY IN THE ORCHID *CALYPSO BULBOSA* (ORCHIDACEAE)[1]

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The lifespan of an individual flower is often affected by pollination success. Species differ regarding whether male function (pollen removal), female function (pollen deposition), or both trigger floral senescence. We studied senescence in the single-flowered, deceptive orchid *Calypso bulbosa* by manipulating the degree of male and female reproductive success. We found that deposition of any amount of pollen resulted in dramatic changes in shape and color within 4 d, whereas unmanipulated flowers and those that had had pollinia removed remained unchanged for 8–11 d after treatment. Selection may favor the reproductive function that is less easily satisfied as the trigger for senescence, because a flower that senesces after accomplishment of this function is likely to have already succeeded at the more easily satisfied one. Deceptive (i.e., rewardless) flowers are more likely to satisfy male than female function since the latter requires that a pollinator be fooled twice, first to pick up pollen and second to deposit it. A survey of naturally pollinated *Calypso* showed that male function, pollinium removal, was more likely to occur than female function, deposition (95% vs. 66% of visited flowers); thus floral senescence in *Calypso* is triggered by achievement of the function less likely to succeed. Studies of senescence triggers in species in which female function is more likely to be achieved than male are necessary to further test this hypothesis.

The lifespan of an individual flower, the period during which it is attractive and available to pollinators, can measure from minutes to months (van der Pijl and Dodson, 1966). At the end of its life a flower may change color, halt production of scent or nectar, and its corolla may change orientation, collapse, or abscise (Gori, 1983). Although phylogeny may sometimes be a constraint (Stratton, 1989), in most species flower lifespan is likely to be an adaptive character; however, despite its potential effects on pollinator visitation or level of inbreeding, longevity of individual flowers is seldom incorporated into studies of plant reproductive strategies (Primack, 1985; Stratton, 1989; Ashman and Schoen, 1994).

There are two basic categories of floral longevity based on the value of a senescent flower to the inflorescence. In the first, a plant retains flowers after they cease functioning in male (pollen presentation) or female (pollen reception) roles to maintain the overall attractiveness of an inflorescence's display. In these species, changes in flower form and color may direct a pollinator's attention to flowers within an infloresence that have not been visited (Gori, 1989; Weiss, 1991). Species in the second category have flowers that undergo complete senescence and are not maintained on an inflorescence; here changes in color and form can be interpreted as epiphenomena of the physiological process of senescence. Both categories of floral longevity can be further subdivided according to the causal agent of senescence. First, flowers may have fixed lifespans that are independent of whether male or female pollination functions have been achieved. For example, the Commelinaceae, Convolvulaceae, Pontederiaceae, and Turneraceae have flowers that invariably last only one day (Primack, 1985). On the other hand, flowers may not have a fixed lifespan but rather be subject to pollinator-induced senescence, triggered by deposition or removal of pollen. In this latter group, species differ regarding whether the onset of senescence is determined by female success (pollen receipt) or male success (pollen removal) (e.g., receipt in *Encyclia krugii,* Ackerman, 1989; removal in *Campanula rapunculoides,* Devlin and Stephenson, 1984). Pollinator-induced senescence may allow reallocation of resources to developing seeds (e.g., Harrison and Arditti, 1976) or decrease transpirational water loss and energy costs of maintaining a flower whose usefulness is at an end (Primack, 1985).

How finely tuned is the flower's "decision" to senesce? If senescence occurs regardless of the amount of pollen removed or deposited it may be at the expense of future reproductive success. For example, the orchid *Cleistes bifaria* undergoes senescence only after receiving a large load of pollen (Gregg, 1991), and *Lupinus argenteus* (Fabaceae) senesces only after its pollen has become inviable (Gori, 1989). By manipulating the degree of male and female reproductive success in the orchid *Calypso bulbosa* we tested the sensitivity of this species' decision to senesce.

MATERIALS AND METHODS

Ecology of Calypso bulbosa—*Calypso bulbosa* (Linnaeus) Oakes var. *americana* (R.Br.) is a single-flowered orchid documented to show post-pollination changes (Gori, 1983). It occurs in mossy, coniferous forests across Canada and the northern United States (Peterson and McKenny, 1968). In the Rocky Mountains of Alberta, *C. bulbosa* blooms from mid-May to early July (Proctor, personal observation). Each ramet produces a single long-stemmed leaf and a solitary pendant flower at the top of

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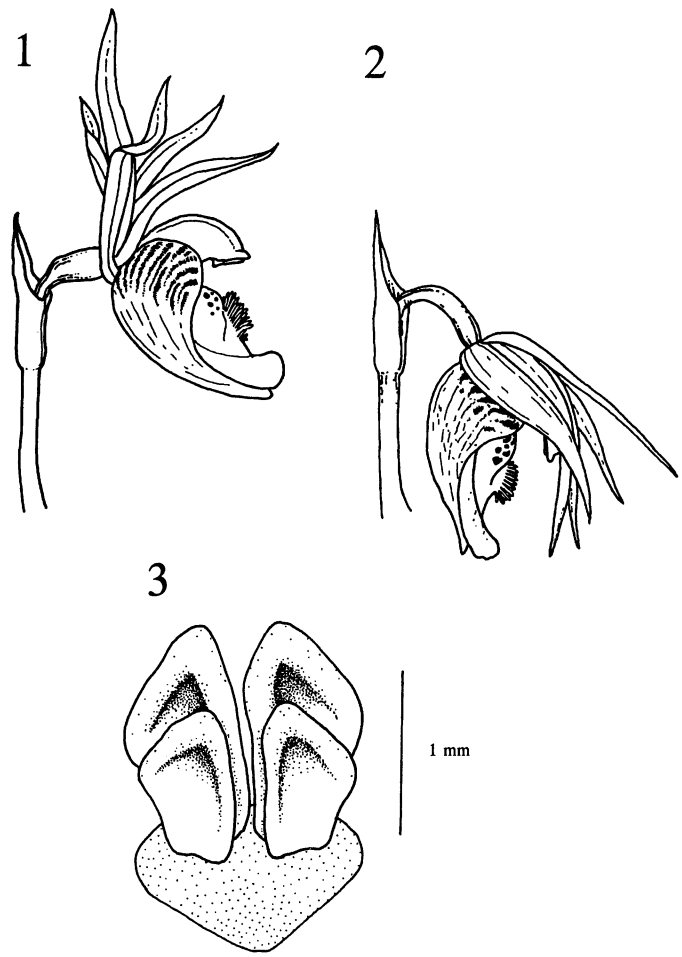
a 5–20 cm stem. The flower has five pink-to-fuchsia sepals and petals, an inflated slipper-like lower lip bearing purple stripes and a tuft of yellow hairs, and a convex column or "upper lip" with anther and stigma on its undersurface (Fig. 1). The anther bears a pollinarium consisting of two pairs of flat, waxy pollinia (one small and one large pollinium per pair) that are attached to a common sticky base (Fig. 3). *Calypso bulbosa* provides neither nectar nor usable pollen; instead it relies on bright color, anther-like hairs, and sweet smell to deceive naive pollinators, mainly queen *Bombus* and *Psithyrus* bumblebees (Mosquin, 1970; Boyden, 1982). A visiting bee removes the entire pollinarium when the viscidium attaches to its thorax, and if it is carrying a pollinarium from another flower it may deposit one, two, three, or four pollinia on the flower's stigma (Proctor and Harder, 1994).

Pollination and floral lifespan—We studied *Calypso* in May 1993 near the University of Calgary's Kananaskis field station in the foothills of Alberta's Rocky Mountains (115°03′N, 51°01′W). Starting 7 May we bagged unopened flowers to preclude pollinator visits. Emasculation was unnecessary because *Calypso* does not self-pollinate (Mosquin, 1970; Proctor, personal observation). After a flower opened and its sepals and petals were fully erect (Fig. 1), we subjected it to one of five treatments chosen to span the range of male and female pollination success. For control (CONT) flowers, pollen was neither removed nor deposited. Flowers with pollinia removed (REM) had the pollinarium and anther cap removed, but received no pollen. We used two pollen loads for treatments involving pollinium deposition: 1/2-DEP flowers were pollinated with one-half of a small pollinium taken from another flower at least 5 m away (the flower's own pollinarium was not removed); 2-DEP flowers were treated similarly to 1/2-DEP but were provided with one small and one large pollinium. Finally, 2-DEP, REM flowers received one large and one small pollinium and had their own pollinaria removed. We chose these levels of pollen deposition because we had previously found that one-half of a small pollinium (1/2-DEP) is insufficient to pollinate all ovules available, fertilizing on average 5,000 seeds compared to the 16,000 fertilized by the one large, one small treatment (2-DEP) (Proctor and Harder, 1994). Thus the 2-DEP treatment would satisfy female function more completely than 1/2-DEP. Flowers were treated between 10 a.m. and 3 p.m. on 10 May ($N = 1$), 11 May ($N = 7$), 12 May ($N = 10$) and 13 May ($N = 4$) for a total of 22 replicates of the five treatments. Flowers were kept bagged and color and morphology were monitored daily after treatment until 21 May (8–11 d after treatment, with the day of treatment considered Day 1). We monitored color of sepals and petals by comparing them to an assortment of Prismacolor® pencils (Berol®, Toronto), and recorded floral morphology by sketching a side view of each flower to indicate the attitude of the lower lip to the stem and that of sepals and petals to the column and lower lip.

Survey of natural pollination success—On 20 May we surveyed unmanipulated *C. bulbosa* in the field station vicinity to determine natural rates of male and female pollination success by checking whether flowers had pollinaria removed or pollinia deposited on their stigmas.



Figs. 1–3. *Calypso bulbosa* flowers and pollinarium. **1.** Lateral view of Stage I flower. **2.** Lateral view of Stage V flower. **3.** Front view of pollinarium showing the two pairs of pollinia attached to a common viscidium.

Viability of pollen from senesced flowers—To determine whether pollinia from flowers that had undergone morphological and color changes could still (a) elicit changes in other flowers, and (b) fertilize ovules, we removed pollinaria from five senesced 2-DEP flowers on 18 May and placed them on stigmas of five flowers that had been bagged prior to their opening. On 24 May we checked the recipient flowers for signs of color and morphological change, and on 16 July we collected and dissected capsules to determine whether seeds had been fertilized.

RESULTS

Course of morphological and color changes—*Calypso bulbosa* flowers underwent a series of morphological and color changes following pollination (Table 1). A flower with originally erect sepals and petals and an ovary that projected out from the stalk (Stage I) gradually developed a drooping ovary that approached the stalk, and sepals and petals that collapsed over the column and lip (Stage V) (Fig. 2). Eventually, as the ovary swelled, the flower rose again until it stood at right angles to the stalk, but

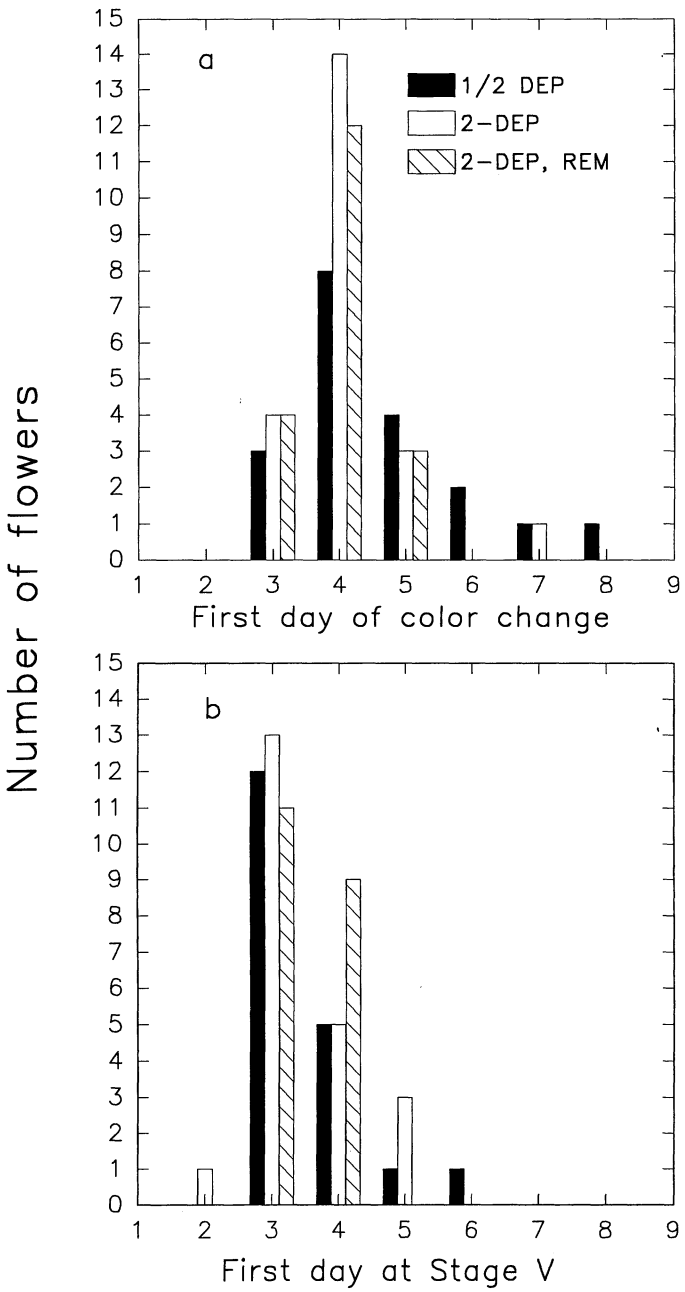


Fig. 4. First day at which pollinated *Calypso* flowers reached (a) Color 3 and (b) Stage V for 1/2-DEP (solid bars), 2-DEP (open bars), and 2-DEP, REM (hatched bars) treatments.

its petals and sepals remained collapsed over the lip (Stage VII). Most pollinated flowers passed from Stage I to Stage III or IV before reaching Stage V, with some passing through II and others going directly to V. By the end of the observation period, approximately half of the pollinated flowers had reached Stage VII. Color change also went through several temporal stages. Initially sepals and petals varied in color from pink to fuchsia (Color 0). Post-pollination color change typically involved a gradual fading to a pale mauve (Color 2), occasionally passing through a stage in which the tips of sepals and petals were Color 0 but their bases were 2 (termed Color 1). Finally, Color 3 was a pinkish orange tone that manifested soon before or after complete collapse of the flower (Stage V).

TABLE 1. Morphological changes in 62 pollinated *Calypso* flowers. Although the order of change was the same for all flowers, some flowers skipped one or more stages.

Stage	Description	Number of flowers
I	Ovary at ≥90° in relation to stem, sepals about 90° in relation to column	62
II	Ovary partially collapsed towards stem, sepals 90°; *or* sepals partially collapsed towards column, ovary 90°	11
III	Ovary partially collapsed, sepals partially collapsed	26
IV	Ovary completely collapsed, sepals partially collapsed	22
V	Ovary completely collapsed, sepals completely collapsed	59
VI	Ovary beginning to rise, sepals completely collapsed	24
VII	Ovary ≥90° again, sepals collapsed	34

Effect of treatments on rapidity of changes—Pollen receipt, but not pollen removal alone, almost invariably induced floral senescence. All of the 21 surviving control flowers retained their initial color and morphology (Color 0, Stage 1) throughout the 8–11 d observation period. Similarly, all but two of the REM flowers remained Color 0, Stage 1 ($N = 22$); the two exceptions developed Color 3 and collapsed sepals and petals on Days 5 and 9, respectively. In contrast to pollinated flowers, however, the ovaries of these two REM flowers did not decline towards the stems. Fifty-nine of 62 flowers in the three treatments involving pollen deposition attained complete morphological collapse (Stage V) and color change (Color 3) by the end of the observation period (Fig. 2). Two of the exceptions also exhibited complete morphological change, but their color changed less dramatically (to Color 2). The remaining exception, a 1/2-DEP flower, remained in initial condition; it seems likely that the small piece of pollinium failed to adhere to the stigma. For plants that received pollen, the amount of pollen applied did not significantly affect either the rapidity of onset of color change (Fig. 4a: Kruskal-Wallis $H = 3.39$, $P > 0.1$), or the rapidity of morphological change (Fig. 4b: $H = 0.118$, $P > 0.5$).

Natural pollination success—Of 520 *C. bulbosa* flowers examined, 212 (41%) showed evidence of having been visited by a pollinator: 11 (2%) had only pollinia deposited, 72 (14%) had only pollinia removed, and 129 (25%) had pollinia both deposited and removed. Thus of visited flowers, 201 (95%) had pollinia removed and 140 (66%) had pollinia deposited.

Viability of pollen from senescent flowers—All five *C. bulbosa* pollinated with pollinia from senescent flowers had reached Color 3, Stage V when reexamined 7 d later. We stained and examined a subsample of seeds (312 to 429) from each capsule and found that more than 98% contained embryos.

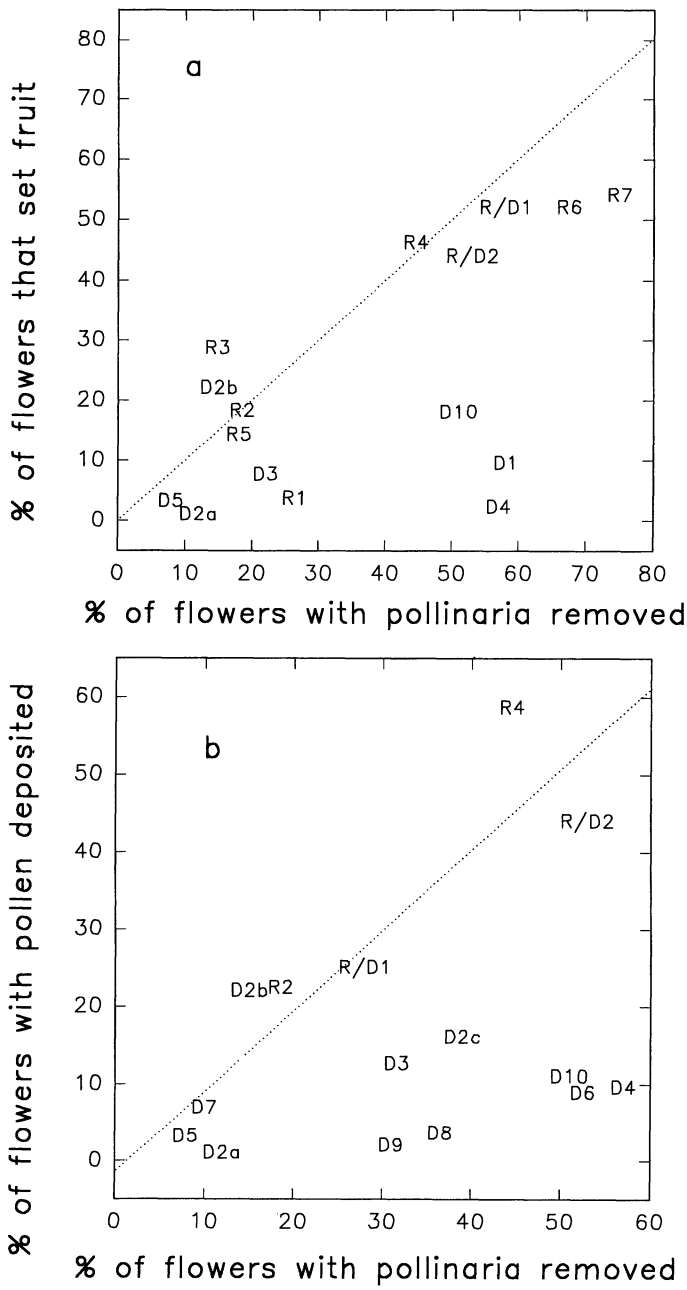


Fig. 5. Comparison of male and female reproductive success in rewarding (R), deceptive (D) and mixed-strategy (R/D) orchids where the dotted line indicates equal success: (a) % of flowers with pollinaria removed vs. % that set fruit; (b) % of flowers with pollinaria removed vs. % with pollen deposited.

Figure Abbreviations: R1 = *Anacamptis pyramidalis,* Waite, Hopkins, and Hitchings, 1991; R2 = *Comparettia falcata* (means over 2 yr), Rodríguez-Robles, Meléndez, and Ackerman, 1992; R3 = *Dactylorhiza fuchsii,* Waite et al., 1991; R4 = *Goodyera oblongifolia,* Ackerman, 1975; R5 = *Habenaria obtusata,* Thien and Utech, 1970; R6 = *Platanthera stricta,* Patt et al., 1987; R7 = *Prasophyllum odoratum,* Bernhardt and Burns-Balogh, 1986; D1 = *Aspasia principissa,* Zimmerman and Aide, 1989; D2a = *Calypso bulbosa,* Boyden, 1982; D2b = *Calypso bulbosa,* Mosquin, 1970; D2c = *Calypso bulbosa,* this study; D3 = *Epidendrum ciliare,* Ackerman and Montalvo, 1990; D4 = *Stelis argentata,* Christensen, 1992; D5 = *Thelymitra antennifera,* Dafni and Calder, 1987; D6 = *Cymbidiella flabellata,* Nilsson et al. 1986; D7 = *Cypripedium acaule* (means over 2 yr), Davis, 1986; D8 = *Diuris maculata* (means over six transects), Beardsell et al., 1986; D9 = *Eulophia cristata,* Lock and Profita, 1975; D10 = *Polystachya rosea* (means over three sites), Pettersson and Nilsson, 1993; R/D1 = *Cleistes bifaria* (means over 2 yr), unpublished data, K. Gregg, Wesleyan College; R/D2 = *Cleistes divaricata* (means over 2 or 3 yr), K. Gregg, personal communication.

DISCUSSION

Morphological and color changes in *Calypso bulbosa* occurred in response to deposition of pollen on the stigma rather than to removal from the anther, as has also been found for the orchids *Cypripedium acaule* (Primack and Hall, 1990) and *Encyclia krugii* (Ackerman, 1989). In *Cymbidium* species, on the other hand, color changes can be induced by removal of pollinia and anther cap (Woltering, 1990). The speed of onset of changes in *Calypso* did not depend on the amount of pollen deposited; in contrast, the orchids *Cleistes bifaria* and *Leporella fimbriata* fade more rapidly after receiving larger doses of pollen (Gregg, 1991; Peakall, 1989). Why does senescence in these species appear to be more sensitive to pollen load than *C. bulbosa*? Differences in pollen packaging may be the explanation. *Leporella* has mealy pollinia and *Cleistes* produces granular pollen that is dumped on pollinators. In both species it is possible for a pollinator to deposit loads of pollen monads or tetrads far too small to successfully fertilize all available ovules. However, the waxy pollinia of *Calypso* cannot be deposited in a load any smaller than one pollinium, which carries enough pollen to fertilize ≈11,000 ovules (Proctor and Harder, 1994). For *Calypso,* unlike for *Cleistes* and *Leporella,* one deposition can be guaranteed to produce a respectable number of seeds. Thus there may have been no selective pressure to respond differentially to insufficient pollen loads because such loads cannot naturally occur.

In *Calypso,* floral senescence was unaffected by male success. By senescing immediately after receiving pollen irrespective of pollinarium removal, *Calypso* flowers appear to forgo potential reproductive success. Pollination doesn't impair the vigor of a flower's own pollen, as pollinia from Stage V, Color 3 flowers successfully pollinated ovules in other plants. This contrasts with Gori's (1989) finding that color changes in *Lupinus argenteus* (Fabaceae) occur only after pollen has become inviable. Casper and La Pine (1984) also found that changed flowers of *Cryptantha humilis* (Boraginaceae) contained inviable pollen. In a study by Richardson and Stephenson (1989) *Campanula rapunculoides* (Campanulaceae) flowers that experienced rapid rates of pollen removal had a significantly shorter lifespan than those experiencing slower rates. Similarly, Devlin and Stephenson (1984) found that the duration of the staminate phase of *Lobelia cardinalis* (Campanulaceae) was correlated with the amount of pollen remaining in the flower.

Why is floral senescence in *Calypso* triggered only by female success? In general, rapid senescence after success of one function seems risky, as it may preclude success of the other function. We propose that the trigger used may indicate which of the two functions is less easily satisfied, e.g., if pollen removal is likely but deposition rare, then a flower that senesces after deposition will most likely already have had some pollen removed and would

not totally forgo male success. *Calypso bulbosa* is a deceptive species that advertizes rewards to pollinators but does not provide them, a phenomenon common among orchids (Ackerman, 1986). In its initial visit to a deceptive flower, a naive insect may remove pollen but it will not have any to deposit. Insects quickly learn to avoid rewardless flowers (Dukas, 1987; Peakall, 1990; Waddington and Gottlieb, 1990; Weiss, 1991); an insect that has been fooled once and is carrying the pollen of a deceptive flower may be disinclined to revisit that species. Thus in deceptive plants, pollen removal seems more probable than deposition, and a senescence trigger based on female success may be favored. Pollinia deposition was rarer than pollinarium removal in our study population (66% vs. 95% of visited flowers), even though each quadripartite pollinarium has the potential to pollinate four stigmas. This suggests that bees quickly learn that *Calypso* provides no rewards and rarely revisit; pollinia would be removed on the first visit but would not have the opportunity of being deposited. But is the difference in pollinia removal vs. deposition truly a result of pollinator avoidance of deceptive flowers, or is it a general feature of orchids? Fig. 5 illustrates relative success of male and female functions in rewarding (R) and deceptive (D) orchid species, comparing pollinium removal with two aspects of female function: fruit set (Fig. 5a) and pollen deposition (Fig. 5b). With regard to fruit set, rewarding species are more likely to have equal male and female success. Studies of pollen deposition in rewarding species are relatively scarce, and more work is needed before a valid comparison can be made using this measure of female success. Two species, *Cleistes bifaria* and *C. divaricata,* are identified with R/D; they are a mixture of the two strategies in that they provide no nectar and hence are deceptive, but bees in some populations have learned to exploit them as pollen sources. Interestingly, they fall closer to the R than the D taxa on Fig. 5.

According to our hypothesis and the pattern in Fig. 5, deceptive orchids should be more likely than rewarding ones to rely solely on female success as a trigger for senescence. Unfortunately, there have been no investigations of rewarding orchids to determine whether pollinium removal affects floral lifespan. Comparative studies of life history and pollination biology are necessary to test whether the relative probability of male vs. female success is responsible for observed patterns of pollinator-induced floral senescence in orchids and other flowering plants.

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